EXPERIMENTAL STUDIES OF SOCIAL FORAGING IN BUDGERIGARS, *MELOPSITTACUS UNDULATUS*

Alice Cowie

A Thesis Submitted for the Degree of PhD
at the
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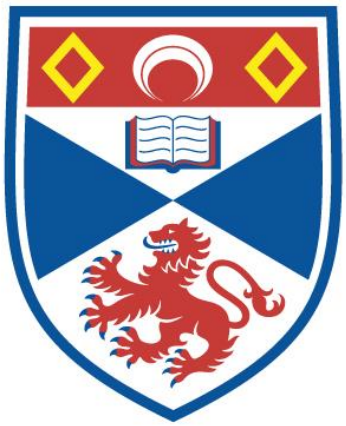

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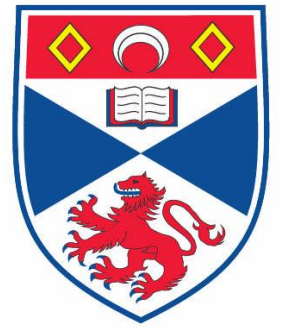

University of St Andrews

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CONTENTS

GENERAL ABSTRACT

Many animals are social foragers. Foraging with others may confer a number of advantages, but is also likely to present a number of challenges that are not encountered by solitary foragers. For instance, whilst feeding in a group may interfere with an animal's ability to learn new foraging skills or the location of new foraging patches by itself, it may simultaneously provide it with the opportunity to acquire new skills or knowledge by means of social learning. This thesis addresses a number of questions relating to the interaction between social foraging and social learning using small groups of captive budgerigars, *Melopsittacus undulatus*, as a test species.

In particular, it investigates the spread of novel foraging behaviour through groups of birds under conditions that either permit or restrict a high degree of 'scrounging' (food stealing) by naïve birds from skilled 'producers' in their group (Chapter Three). Scrounging is found to inhibit naïve budgerigars' performance of new foraging skills, but appears to facilitate their underlying acquisition, or motivation to acquire these skills, when the need arises – for instance, when producers are lost from their group. In addition, the thesis assesses the importance of a number of different individual-level characteristics, such as age, sex, and competitive rank, in predicting birds' propensity to behave as producers rather than scroungers when foraging in a group (Chapter Four).

The thesis also examines budgerigars' relative use of social and personal information when selecting foraging locations (Chapter Five), and assesses the importance of group social networks in predicting individual birds' order and latency to arrive at

foraging patches (Chapter Six). Budgerigars are found to rely on social information when they lack any personal information about foraging locations. When equipped with both social information and personal information, some, but not all birds appear still to utilise social information. Birds' social networks appear to have little bearing on individuals' foraging patch visitation times.

CHAPTER ONE

GENERAL INTRODUCTION

Social Foraging: Opportunities and Constraints

Many animals forage in groups (Clark and Mangel, 1986; Giraldeau and Caraco, 2000; Krause and Ruxton, 2002). This may confer a number of advantages, but is also likely to present a number of challenges that are not encountered by solitary foragers. For instance, group foraging can bring benefits in terms of reduced predation risk (e.g. Banks, 2001; Sorato *et al.*, 2012) and increased foraging efficiency (e.g. Pitcher and Magurran, 1982; Travers, 1993). However, it can also result in competition over limited resources (e.g. Stolen et al, 2012; van Dijk et al, 2012).

Feeding in a group may interfere with an animal's ability to learn new foraging skills, or about the location of new foraging patches, by itself (Giraldeau et al, 1994; Giraldeau and Caraco, 2000). One reason for this is that it may permit naïve animals to exploit the efforts of nearby individuals that have successfully managed to access a food source. This may cause a reduction in the time naïve animals devote to personal exploration of an area, or to the acquisition of skills necessary to extract or process a given food item. Moreover, it may cause them to develop associations between the presence of other animals and the availability of food that interfere with their ability to develop associations between personal exploration and manipulation of items, and obtaining a food reward (e.g., Beauchamp and Kacelnik, 1991). In addition, proficient foragers in a group may deplete the food available at a particular location, further reducing the likelihood of naïve animals learning to associate individual exploration with resultant foraging success.

Whilst foraging in the presence of others may compromise individual learning, it may simultaneously potentially provide animals with the opportunity to acquire new skills or knowledge by means of social learning (Heyes, 1994; Nicol, 1995, 2006; Hoppitt and Laland, 2008; Hoppitt and Laland, 2013). Broadly speaking, social learning can be described as learning that is facilitated by observation of, or interaction with, another individual (often, but not always, a conspecific) or its products (adapted from Heyes, 1994; Hoppitt and Laland, 2008, 2013). Several different social learning 'mechanisms' have been proposed by a number of authors (reviewed in Whiten and Ham, 1992; Heyes, 1994; Nicol, 1995; Zentall, 1996; Hoppitt and Laland, 2008, 2013), although there is currently no absolute agreement as to how the phenomenon of social learning should best be categorised. The processes so far suggested (see next section for an overview) do not form any obvious hierarchy, are not necessarily mutually exclusive, and may lead to learning either by direct or indirect means (Hoppitt and Laland, 2008, 2013).

It is possible that using information provided by others may spare an animal the time and energy costs involved in individual trial-and-error learning and equip it with a 'short-cut' to acquiring adaptive information (Galef, 1995; Laland, 2004). At the very least, social learning may serve to mitigate the inhibitory effects of group foraging on individual learning (Giraldeau et al, 1994; Giraldeau and Caraco, 2000). A group foraging animal, for example, may be able to learn about the location of profitable food sources (and subsequently exploit these patches itself) by monitoring the activities of other animals in its group (e.g. Wilkinson, 1992; Templeton and Giraldeau, 1996; Coolen et al, 2003; Kendal et al, 2004). It may also be able to acquire social information about potential new food types (e.g. Galef, 1996; Sherwin

et al., 2001) or potential poisons (e.g. Mason *et al.*, 1984; Fryday and Grieg-Smith, 1994; Johnston *et al.*, 1998). Note, however, that acquiring social information about potential novel food sources may not involve the same cognitive processes as acquiring social information about food sources that are dangerous, and that animals may be capable of one form of social information use but not the other. For instance, when naïve Norway rats, *Rattus norvegicus*, interact with a recently fed conspecific, they exhibit a substantial enhancement in their preference for the food eaten by the conspecific (Galef and Wigmore, 1983). This remains the case even when the conspecific is unconscious or experiencing acute gastrointestinal distress (Galef *et al.*, 1983), which suggests that the social transmission of food preferences in rats functions to help them identify potential foods, rather than to aid in their identification of potential poisonous food substances – perhaps because wild Norway rats rarely encounter toxic food, or are usually unlikely to interact with one another following the consumption of such items (Noble *et al.*, 2001). In domestic chickens, *Gallus gallus domesticus*, meanwhile, social learning of avoiding noxious substances occurs in chicks (Johnston *et al.*, 1998) but not in adults (Sherwin *et al.*, 2001). In this and probably many other species, social learning of aversions may confer greater benefit to young animals that have not had time to develop experience of foods, than it does to adults (Sherwin *et al.*, 2001).

Furthermore, group foragers may be able to exploit social information in order to acquire new foraging skills. This may be particularly useful in the case of complex skills, for instance involving tool use, which animals may be very slow to acquire, or unlikely to acquire at all, by means of individual trial-and-error learning, on account of a single individual being highly unlikely to stumble upon the exact sequence of

actions required to accomplish the task in question (e.g. Day *et al*., 2003; Whiten *et al*., 2005; Thornton and Malapert, 2009).

In this thesis, I aim to investigate the relationship between social foraging and social learning using small groups of captive budgerigars, *Melopsittacus undulatus*. Specifically, I intend to assess birds' acquisition and utilisation (a) of novel foraging skills, and (b) of information about the location of novel foraging patches when in groups. Before investigating this, however, it is important to familiarise the reader with some key concepts in social learning research. These include the psychological mechanisms used in social learning, and the strategies employed when individuals choose whom and when to copy.

Social Learning Mechanisms

A number of potential mechanisms by which animals may to be able to learn from others are currently recognised. These include any kind of direct, or indirect, process that can lead to social learning (Hoppitt and Laland, 2008, 2013). As previously stated, these mechanisms do not form any obvious hierarchy and are not necessarily mutually exclusive (Hoppitt and Laland, 2008, 2013). Indeed, it is often difficult, if not impossible, to tease apart empirically which exact mechanism(s) an animal is employing, since its behaviour may be consistent with several alternatives (Hoppitt and Laland, 2013). For a (non-exhaustive) summary of the empirical evidence available for each of the mechanisms reviewed in this section, see Table 1.1.

Table 1.1: Current empirical evidence for eight different social learning mechanisms; alternative mechanisms consistent with current evidence; and potential methodological refinements to improve mechanism detection.

Mechanism	Empirical Evidence (Birds)	Empirical Evidence (Other Species)	Alternative Mechanisms Consistent with Current Empirical Evidence	Potential Methodological Refinements to Aid Mechanism Detection
Stimulus Enhancement	• Great tits more likely to interact with a particular 'type' of place to get food after seeing conspecific find food in a similar type of location (Krebs *et al.*, 1972) • 'Mate-choice copying' in female quail (Galef and White, 1998)	• 'Mate-choice copying' in female guppies (Dugatkin and Godin, 1993)	• Observational Conditioning	• Do not reward demonstrator for actions (e.g., Fritz *et al.*, 2000) • Use a model demonstrator (e.g., Leadbeater and Chittka, 2007)
Local Enhancement	• Budgerigar foraging choices (Heyes and Saggerson, 2002) • Lid-opening in greylag geese (Fritz *et al.*, 2000)	• Flower-colour reversal learning in bumblebees (Leadbeater and Chittka, 2007)	• Observational conditioning	• Do not reward demonstrator for actions (e.g., Fritz *et al.*, 2000) • Use a model demonstrator (e.g., Leadbeater and Chittka, 2007)
Food Preference Enhancement	• Hens (Sherwin *et al.*, 2001)	• Norway rats (Galef and Wigmore, 1983)		
Observational Conditioning	• Great tits learning feeding-site locations (Krebs *et al.*, 1972) • Blackbird predator recognition (Curio, 1988)	• Rhesus monkeys snake fear response (Cook *et al.*, 1985)	• Stimulus enhancement	• Do not reward demonstrator for actions (e.g., Fritz *et al.*, 2000) • Use a model demonstrator (e.g., Leadbeater and Chittka, 2007)

Observational Response-Stimulus Learning	• Novel foraging task solving in pigeons (Palameta and Lefebrve, 1985; Giraldeau and Templeton, 1991) • Pigeon treadle-pecking/stepping devaluation test (Saggerson *et al.*, 2005)		• Observational conditioning / contextual imitation	• Modified two-action task in which observer sees a demonstrator respond to same contextual stimulus with two actions, one rewarded and one unrewarded (Hoppitt and Laland, 2013) • Devaluation procedure (e.g., Saggerson *et al.*, 2005)
Contextual Imitation	• Two-action tasks with budgerigars, (Dawson and Foss, 1965), pigeons (Zentall *et al.*, 1996; Kaiser *et al*, 1997) and quail (Akins and Zentall, 1996)		• Response facilitation	• Introduce a delay filled with another observed or performed activity between observation and performance of a task to let effects of response facilitation wear off (Hoppitt and Laland, 2013) • Introduce control subjects who do not observe demonstrators solving tasks, but instead observe them performing the same actions in a different context (Hoppitt and Laland, 2013)
Production Imitation	• Movement imitation in an African grey parrot (Moore, 1992)	• Chimpanzee artificial fruit opening (Whiten, 1998) • "Do-as-I-do" experiments on chimpanzees (Hayes and Hayes, 1952; Custance *et al.*, 1995) and orangutans (Call, 2001)	• Emulation • Contextual imitation / response facilitation (difficult to rule out possibility that actions may already be part of subjects' gestural repertoire, as found by Byrne and Tanner, 2006, in a study on western lowland gorillas)	• Detailed motion analysis of motor patterns used by demonstrators and observers (Voelkl and Huber, 2007)
Emulation	• Screen-pushing by pigeons following a ghost demonstration (Klein and Zentall, 2003)	• Bar-pushing by rats following a ghost demonstration (Denny *et al.*, 1983, 1988)	• Stimulus enhancement	• Design an apparatus that can be manipulated in numerous different ways to achieve the same end result (Hoppitt and Laland, 2013)

The ‘simplest’ social learning mechanisms currently recognised – often deemed to be the least cognitively demanding (Hoppitt and Laland, 2008) – are ‘stimulus enhancement’ (Spence, 1937) and ‘local enhancement’ (Thorpe, 1963). The first occurs when a ‘demonstrator’s’ (knowledgeable individual’s) behaviour increases the likelihood of an ‘observer’ (naïve individual) being exposed to a stimulus, and of its subsequently learning to interact with similar stimuli in future. The second occurs when a demonstrator’s interactions with objects at a particular location increase the probability of an observer visiting or interacting with (and thus learning about) objects at that location. It is sometimes considered a sub-type of stimulus enhancement when the stimulus in question is a location (Heyes, 1994 – but see Hoppitt and Laland, 2008). Another very specific form of social learning, and one that, like local enhancement, appears to be widespread in nature, is the ‘social enhancement of food preferences’ (Galef, 1989), whereby an animal becomes more likely to consume a particular food after encountering a demonstrator bearing cues associated with the food.

Another form of social learning is ‘observational conditioning’, defined by Heyes (1994) as a sub-set of stimulus-stimulus learning in which observation of a demonstrator allows an individual to learn about the relationship between two stimuli, and causes it to alter its behaviour in some way at a later time. Numerous instances of social transmission can potentially be accounted for by observational conditioning, including cases when an observer learns where to find food after observing a demonstrator foraging, conceivably by learning to associate environmental cues with food (e.g. Krebs *et al.*, 1972; McQuoid and Galef, 1993). Such examples, however, are also consistent with other processes such as stimulus enhancement (Hoppitt and

Laland, 2013). Less ambiguous occurrences of observational conditioning include the social transmission of snake fear in rhesus monkeys, *Macaca mulatta* (Cook *et al.*, 1985) and the social transmission of predator recognition in blackbirds, *Turdus merula* (Curio, 1988). In both cases, individuals that have had no previous contact with the predator in question exhibit no fear when presented with it. If, however, they are exposed to another individual reacting fearfully to the predator, they too will display fear, and will again display fear when later presented with the predator on its own.

'Observational response-stimulus learning' (Heyes, 1994; Hoppitt and Laland, 2008) occurs when observation of a demonstrator exposes an observer to the relationship between a response and a reinforcer and results in some change in its behaviour at a later point in time. To demonstrate observational response-stimulus learning, it is necessary to show that an observer has formed an association between the action it saw a demonstrator perform and the observed consequences of that action. When the observed consequences of the action are favourable, the observer will be more likely to perform the same action in the same context (Hoppitt and Laland, 2013). In order to distinguish experimentally between observational response-stimulus learning and observational conditioning, as well as response facilitation and contextual imitation (see below), Saggerson *et al.* (2005) devised a 'devaluation' procedure to test for the formation of response-stimulus associations in naïve pigeons, *Columba livia*. Observers watched demonstrators stepping on treadle to receive a reward of grain lit by a red light, and pecking at the same treadle to receive a reward of grain lit by a green light (or vice versa). Devaluation training, in which birds received separate presentations of each light, one paired with food and the other not, was then given.

When observers were subsequently given access to the treadle, they preferentially responded with the action they had observed leading to the non-devalued outcome, suggesting that they had indeed formed an association between an action and its outcome through observation.

Another proposed social learning mechanism is 'imitation'. This can be broken down into two sub-categories, 'contextual imitation' and 'production imitation' (Byrne, 2002). The former involves an observer seeing a demonstrator perform an act in a specific context, which subsequently makes it more likely to perform the same act in the same context. The latter involves an observer seeing a demonstrator perform a novel act, sequence of acts, or combination of acts, and subsequently becoming more likely to perform that new act or sequence of acts itself. Contextual imitation is generally regarded as a form of stimulus-response learning. Production imitation, however, is different from response-stimulus learning, because in addition to learning about the consequences of a response, it involves learning by observation how to perform that response. In addition, Byrne and Russon (1998) suggest that animals may sometimes exhibit different 'levels' of imitation. For instance, an 'imitator' may not always need to copy every exact movement made by its demonstrator, but may rather extract the underlying organisation of its behaviour and replicate that ('program-level imitation' as opposed to 'action-level imitation'). Program-level imitation differs from merely imitating at a low level of resolution, since it requires inferences about which aspects of a sequence are important. In practical terms, however, the two are likely to be almost impossible to differentiate (Hoppitt and Laland, 2013).

A further proposed social learning mechanism is ‘emulation’. This occurs when, following observation of a demonstrator interacting with objects in its environment, an observer becomes more likely to perform any actions that bring about a similar effect on those objects (Hoppitt and Laland, 2008). It is possible that emulation could occur when an observer not only understands that its demonstrator’s behaviour has certain outcomes, but that these same outcomes may be achieved by means of alternative actions (‘goal emulation’ – see Whiten and Ham, 1992). Alternatively, and perhaps more simply, an observer might learn to copy the results of a demonstrator’s actions (rather than its actual actions, as in the case of imitation) by ‘object movement re-enactment’, whereby it might try to re-create the movements of objects with which the demonstrator interacted; or ‘final state re-creation’, whereby it might try to re-create the final (or even an intermediate) state resulting from a demonstrator’s behaviour (Custance et al, 1999). In practical terms, emulation can be difficult to differentiate from potentially simpler mechanisms of social learning (low-resolution imitation, or stimulus enhancement), which can produce outwardly similar behavioural responses in observers. Imitation can potentially be ruled out by exposing observers to disembodied, or ‘ghost’, movements of an experimental apparatus and testing whether they recreate the movements they observe (Whiten and Ham, 1992) even though unable to observe a demonstrator’s body movements. If an apparatus is designed such that it can be manipulated in numerous different ways to achieve the same end result, it may also be possible to distinguish emulation, which would involve recreation of the particular manipulation demonstrated, from simple stimulus enhancement, which need not do (Hoppitt and Laland, 2013).

Two final mechanisms that can result indirectly in learning are 'social facilitation' (Zajonc, 1965) and 'response facilitation' (Byrne, 1994). Social facilitation occurs when the mere presence of a demonstrator influences an observer's behaviour (Zajonc, 1965), and can potentially lead indirectly to learning if, for instance, an individual becomes more likely to engage in exploratory behaviour in the presence of other individuals, perhaps due to a reduction in neophobia, which may then allow it to learn about novel objects. Hoppitt and Laland (2013) point out that social learning researchers' main interest in social facilitation is as a process that must be ruled out before any 'true' social learning mechanisms can be inferred – i.e., one must run control experiments to ascertain that it is not just the mere presence of a conspecific, but rather some aspect of its activity, that is responsible for a naïve observer's increased rate of acquisition of a trait. Response facilitation occurs when the sight of a demonstrator performing an act encourages an observer to engage in it as well (Byrne, 1994). It is generally assumed to have only a transient effect on behaviour, because the effect may be caused by the priming of brain records corresponding to an action, with residual neural activity remaining for a short time after observation of a demonstrator's actions (Byrne, 1994). Though not a learning process itself, response facilitation can potentially result in learning if an observer receives some kind of reinforcement from its actions. Unlike production imitation, response facilitation involves observers exhibiting behaviours that are already in their repertoire; and unlike contextual imitation (during which observers learn to employ an action in specific, novel circumstances), animals exhibiting response facilitation will perform an action irrespective of context. Response facilitation and contextual imitation, however, can be very difficult to distinguish empirically. For example, Zentall *et al.* (1996) devised a two-action experiment in which naïve observer pigeons saw a

demonstrator either peck or step on a treadle to obtain a food reward, and found that observers were more likely to solve the task using the method they had seen demonstrated when presented with the treadle themselves. Since both pecking and treading actions were directed to the same location and resulted in the same movement of the treadle, the authors were able to rule out local enhancement and emulation as potential explanations for their findings, and concluded that their observer pigeons had engaged in contextual imitation. Byrne (1999, 2002), however, argues that response facilitation provides an alternative explanation for these results, with observers that saw a demonstrator peck perhaps being more likely to peck when themselves tested on the task, on account of a transient increase in pecking rate (or the probability of pecking) in relation to stepping. Hoppitt and Laland (2013) propose that one way of eliminating response facilitation as an explanation could be to introduce a delay filled with another observed or performed activity between observation and performance of a task, to let the possible effects of response facilitation wear off; or to introduce control subjects who do not observe demonstrators solving tasks, but instead observe them performing the same actions in a different context.

Social Learning Strategies

A common assumption (though one which is rarely made explicit) among ethologists, ecologists, behavioural ecologists, and anthropologists, is that social learning is inherently adaptive (Laland, 2004; Kendal et al, 2005), since it may provide animals with a short-cut to acquiring information and spare them the costs of having to learn for themselves by trial and error.

Though intuitively appealing, the argument is fundamentally flawed. This is because social learners are essentially 'information parasites' living at the expense of the rest of their population, exploiting the information, skills, and resources acquired, devised or discovered through others' individual (asocial) learning, but contributing no new information themselves. In the extreme scenario of a population exposed to a changing environment where every individual acted as a parasite, and never learnt anything for itself, a point would eventually be reached whereby all individuals were performing outdated modes of behaviour no longer suited to their current environment. At this point, far from being advantageous, 'copying' would clearly be maladaptive (Boyd and Richerson, 1985, 1995; Rogers, 1988; Giraldeau *et al*., 2002).

In order for social learning to constitute an 'evolutionarily stable strategy', then, either some individuals in the population must be consistent information 'generators' and rely exclusively on asocial learning or, more realistically, individuals must use social learning discriminatively and sample the environment directly through their own asocial learning some of the time (Galef, 1995). Natural selection ought to have favoured 'transmission biases' or specific adaptive social learning 'strategies' that dictate the contexts under which individuals will rely on information provided by others, instead of learning by themselves (Boyd and Richerson, 1988). Animals should be selective with regard to when, and from whom, they use social information, and what they learn (Laland, 2004; Hoppitt and Laland, 2013). For instance, when personal interaction with the environment involves substantial costs, either in the form of direct risks to survival (from injury, poisoning, or predation), or 'lost opportunity' costs (where time or energy could be spent elsewhere), theoretical analyses reveal that natural selection should favour copying others (Boyd and Richerson, 1985; Feldman

et al., 1996). Social learning may also be favoured when an individual is for some reason 'uncertain' as to how best to behave – perhaps because it is young and lacks any relevant prior knowledge to guide its decision making, or because it lacks up-to-date information about a situation (Kendal *et al*., 2005).

Animals may also place greater reliance on the information provided by particular individuals over others. Coussi-Korbel and Fragaszy (1995) introduced the concept of 'directed social learning', suggesting that the probability of an animal learning from a given demonstrator may be critically affected by the demonstrator's identity (for instance, whether it is kin or non-kin, familiar or unfamiliar, 'friend' or 'foe') and characteristics (such as its age, social status, sex, and proximity to the observer). Laland (2004) also suggests that animals may exhibit such strategies as 'copy the majority', or 'copy successful individuals'.

There exists a growing body of empirical evidence for animals' use of a range of different social learning strategies (reviewed in Rendell *et al.*, 2011; Hoppitt and Laland, 2013). The number of studies, however, that have so far been conducted on any one given strategy, such as copy when uncertain, remain relatively few (and are restricted to a handful of species). For instance, copy when uncertain strategies have thus far been explicitly tested only in Norway rats (Galef 1996, 2009) (naïve but not experienced rats copy the diet preferences of conspecifics); guppies, *Poecilia reticulata* (Kendal *et al.*, 2004) and sticklebacks, *Pungitius pungitius* (van Bergen *et al.*, 2004) (naïve but not experienced fish prefer to visit the same food sites as conspecific demonstrators); and black ants, *Lasius niger* (Grüter *et al.*, 2011) (naïve individuals being more likely than experienced ones to follow the chemical trails of

conspecifics). As such, this emerging field of interest remains ripe for further empirical testing. Nomadic, group foraging birds such as budgerigars are highly likely to encounter novel foraging situations in which paying attention to the location and activities of others in their flock may improve their foraging efficiency or reduce their risk of predation. They therefore represent a useful test species in which to conduct additional experimental tests of a number of social learning strategies.

This Study

In the following chapters, I investigate several questions regarding the relationship between social foraging and social learning using small (ranging in size from seven to fourteen individuals), freely-interacting, mixed-sex, mixed-age groups of captive budgerigars. (For more details on budgerigars, and why they were selected for this study, see Chapter Two).

In Chapter Three, I investigate budgerigars' ability to solve a number of different novel foraging tasks, and the extent to which new foraging skills, once displayed by one bird, spread to other members of its group. I examine whether social information made available by trained 'demonstrators' (birds already skilled at accessing food from a given foraging task) causes naïve group members to perform novel foraging skills more quickly than when no demonstrator is present in their group. Furthermore, I manipulate the reward that non task-solving birds ('scroungers') are able to obtain through stealing food from tasks that have been solved by other members of their group ('producers'), and assess what effect this has on naïve birds' performance of

novel foraging skills. Previous studies of the impact of scrounging on naïve animals' skill acquisition have varied scrounging opportunities by using physical barriers (Plexiglas screens) to prevent naïve animals from interacting with producers and/or foraging tasks (thus preventing scrounging) during some tests, whilst allowing free mixing of naïve animals and producers (thus permitting scrounging) during others (e.g., Giraldeau and Lefebrve, 1987; Nicol and Pope, 1994). This raises the possibility that differences in naïve animals' uptake of new skills across tests may arise not from differences in the extent to which they were able to scrounge, but, for instance, from differences in their ability to view tasks being solved, or in their experience of aggression from fellow group mates, under barrier / non-barrier conditions. This study extends the work of previous ones by manipulating scrounging opportunities whilst enabling birds to remain under freely-interacting (more naturalistic) group conditions throughout.

In Chapter Four, I explore whether individual birds vary in their propensity to solve novel foraging problems, using data obtained during the presentation of several different foraging tasks to each group of budgerigars in Chapter Three. Theoretical models of the producer-scrounger game tend to assume, perhaps rather unrealistically, that foragers are equally able to use each strategy and that the payoffs they reap from adopting one or the other are independent of characteristics such as their place in a group dominance hierarchy (Beauchamp, 2001). Meanwhile, only a handful of empirical studies have looked for correlations between an animal's behaviour as a producer or a scrounger, and a range of individual traits (most often, its place in the group dominance hierarchy) (e.g. Baker *et al.*, 1981; Barnard and Sibly, 1981; Rohwer and Ewald, 1981; Czikeli, 1983; Beauchamp, 2006). Here, I assess whether

certain birds act as task solvers / producers across the presentation of multiple different tasks, whilst others fail to solve any of them; or whether birds form 'skill pools' (Giraldeau, 1984), with a different sub-set of group members acting as producers for each particular task. In addition, I explore the utility of a number of individual-level characteristics including birds' age, sex, body condition, and competitive rank within their group, in predicting their latency to solve the novel foraging problems presented.

In Chapter Five, the focus of the thesis shifts from examining budgerigars' ability to acquire new foraging skills when in a group, to exploring their potential use of certain social learning strategies when foraging in a group – specifically, 'copy / feed in the same location as others when uncertain' strategies. I investigate their ability to use social information to discover and exploit new foraging patches, and assess whether naïve birds in groups containing trained demonstrators (birds with prior knowledge of a particular foraging patch) typically exploit food patches more quickly than naïve birds in groups that do not contain demonstrators. I also investigate the extent to which birds with prior personal information about the location and accessibility of one food patch rely on social information provided about another patch, which conflicts with their own existing information.

In Chapter Six, I use a newly developed technique, Network-based Diffusion Analysis (*NBDA*), to investigate the importance of individuals' associative relationships in predicting the sequence and timing of birds' arrival at a sub-set of the novel foraging patches presented in Chapter Five. The aim of this is to test one aspect of Coussi-Korbel and Fragaszy's (1995) concept of 'directed social learning', which assumes

that naïve animals may learn, or use social information, preferentially from certain members of their group (for instance close affiliates) over others.

The thesis ends with a general discussion (Chapter Seven), which draws out the principal take-home messages from the study.

CHAPTER TWO

ECOLOGY AND BEHAVIOUR OF BUDGERIGARS, *MELOPSITTACUS UNDULATUS*, AND THEIR USE IN BEHAVIOURAL STUDIES

Evolutionary History, Ecology and Behaviour

Budgerigars, *Melopsittacus undulatus*, also known as parakeets, or shell parakeets, are small parrots native to Australia. The only members of the genus *Melopsittacus*, recent phylogenetic studies reveal them to be closely related to lories (subfamily Loriinae) and fig parrots (tribe Cyclopsittacini) (Schweizer *et al*., 2010).

Wild adult budgerigars are approximately 18 cm long and have a body mass of 30-40 g, with light green abdomens, black and yellow wings, yellow faces and blue tails (Forshaw and Cooper, 1978). Domesticated populations, however, exhibit considerable variation in both size and plumage (Radke, 1988). Males and females are monomorphic except for their ceres (facial area containing the nostrils), which become royal blue in males, but which are pale brown and dark brown in non-breeding and breeding females, respectively (Forshaw *et al*., 1978; Baltz and Clark, 1996) (Fig. 1). Maximum lifespan in captivity is around 20 years (Holmes *et al*., 2003).

Figure 2.1: Adult female (left) and male (right) wild-type budgerigar.

Budgerigars are social birds, living in flocks throughout the year and performing most of their diurnal activities as part of a group. Flocks exhibit no obvious hierarchical structure, and contain individuals of all ages and both sexes (Wyndham, 1980). Flocks are typically quite small, ranging in size from a few pairs of individuals to a few hundred birds, but may become greatly enlarged (numbering several thousand individuals) when food and water is locally abundant (Forshaw and Cooper, 1978).

Budgerigars are highly nomadic, their movements being determined by the availability of food and water. They primarily occupy eucalyptus scrub and grassland, but are intermittently driven into more wooded or coastal areas during drought (Forshaw and Cooper, 1978; Radtke, 1988; Moravec *et al.*, 2006). Daily activity begins at sunrise and ends at dusk. Most feeding takes place in the morning and

afternoon, though drinking is sporadic and can occur at any time of day. During the midday heat, individuals tend to rest and preen in the branches of trees (Wyndham, 1980).

Budgerigars are seed eaters, feeding on spinifex, grass weeds and sometimes ripening wheat (Forshaw and Cooper, 1978). Males, females and juveniles have similar diets, though whereas adults are able to survive on dried, non-germinated seeds from a previous season, newly-hatched chicks require their parents to provision them with freshly-ripened (easier to digest) grass seeds whilst in the nest (Radke, 1988).

Predators of the budgerigar include other bird species (notably pied butcherbirds, *Cracticus nigrogularis*) and tree snakes (Wyndham, 1980; Radtke, 1988). Whilst their green and yellow plumage provides them with camouflage when resting in eucalyptus trees during the noontime heat (Radtke, 1988), budgerigars are susceptible to predation when feeding on exposed grassland. Foraging in flocks is likely to have evolved as an adaptation to reduce this predation risk (Krebs and Davies, 1993).

Budgerigars are socially monogamous (though opportunistically polygamous – Moravec *et al.*, 2006) and generally form long-term pair bonds (Stamps et al, 1985). Bonds form following courtship, which is typically initiated by males. Initial stages of courtship involve the male warble singing, head bobbing, nudging, head-shaking, and flying or walking towards or away from the female being courted (Brockway, 1964b). Females can be aggressive towards males when unreceptive to their courtship solicitations (Trillmich, 1976). Female head-shaking, however, typically signals to a male that he can approach without risk of physical rebuff (Hile *et al.*, 2005). At this

point courtship progresses to beak-hooking, courtship feeding (regurgitation of seeds, normally by the male to the female) and the mutual displaying of head feathers (Brockway, 1964).

In a study of group-living captive budgerigars, Trillmich (1976) found that once a pair bond had been formed, birds sat together more frequently, and for longer periods of time, than unpaired birds. Mutual preening, beak touching, courtship feeding (regurgitation of seeds, normally by the male to the female – a likely benefit of which may be energy supplementation for the female in advance of egg laying (Helfenstein *et al*., 2003)), adult food begging (normally by the female to the male) and copulation behaviours occurred at a significantly higher frequency among pair bonded birds than among unpaired birds. Within pairs, males were more active than females in maintaining proximity to their partner (males made proportionally more approaches towards, and fewer departures from, their female partner than vice versa). Agonistic behaviour such as beak thrusting (Brockway, 1964b) occurred at a lower rate between pair bonded birds than it did between unpaired birds.

Individuals within a flock form pair bonds outside of the breeding season and subsequently remain together throughout the year (Trillmich, 1976). They are capable of breeding from the age of three to four months onwards, and do so following rainy periods, when food is temporarily abundant. The permanent cohesion of pairs in a flock outside the breeding season may serve to ensure that birds are able to begin breeding with minimal delay (a few days to two weeks) following rainfall, thus achieving maximum reproductive success in the brief period propitious for rearing young (Trillmich, 1976). In order to complete a breeding cycle successfully – from

locating a nest site through to fledging young – budgerigars need two to three months access to a food supply that exceeds their own maintenance requirements. They may otherwise be forced to desert the nest and begin another breeding attempt elsewhere (Wyndham, 1981).

Budgerigars are cavity breeders, and females seek out holes (often in decaying eucalyptus trees) in which to lay their eggs. Hole entrances are ideally between three and six cm in diameter, since these are too small for predatory pied butcherbirds, or sympatric hole-nesting species such as cockatiels, *Nymphicus hollandicus*, mallee ringnecks, *Barnardius barnardi*, or galahs, *Cacatua roseicapilla*, to penetrate. Eggs are laid 0.3-1.5 m away from the cavity entrance, at the bottom of a hollow on a soft mat of decaying wood and faeces. Depending on the availability of suitable nest holes, several budgerigar pairs may nest in the same tree at the same time (Wyndham, 1981).

Unlike males, who arrive at breeding sites with their spermatogenic cycle well advanced, females arrive with undeveloped ovarian follicles (Wyndham, 1980), and a number of stimuli are known to be important in initiating the physiological changes a female must undergo prior to egg-laying. Hutchison (1974) found that captive females would only lay eggs when provided with a nest box or kept in the dark (darkness being a key feature of natural nest cavities). Whilst this alone was sufficient to induce egg production in a few individuals, most required further auditory and visual stimulation from their mates in order to progress to this stage of their reproductive cycle.

Once her follicles are mature (generally around nine days after first moving into a nest hole – Hutchison, 1977), a female will begin laying, typically producing between four and five eggs over the course of a similar number of days. Incubation starts as soon as the first egg has been laid, and continues for a further 17-18 days for each egg. Hatching is therefore asynchronous and spread over a four to five day period (Wyndham, 1981).

Whilst males do periodically enter the nest cavity to feed their mate (Radtke, 1988), it is females who are primarily, if not totally, responsible for incubation and brooding of the eggs (Stamps *et al*., 1985; Moravec *et al*., 2006). During this time, males may pursue extra-pair copulations with other females nesting nearby. Such behaviour can be costly, since it may interfere with a male's ability to guard his own mate (Baltz, 1994), and may disrupt his pair bond with her (in extreme cases leading to permanent separation – Baltz and Clark, 1996). It would therefore be especially unwise for males to attempt to mate with non-fertile extra-pair females that had not yet ovulated. Experimental evidence suggests that they avoid making this mistake by assessing females' cere colours (which vary in accordance with their state of ovarian development, becoming darker brown when they are fertile) and focussing their attentions on individuals that are ready to lay eggs (Baltz and Clark, 1994).

Budgerigar chicks hatch in an altricial state and take approximately 35 days to fledge (Wyndham, 1981). Using a combination of naturalistic observations and laboratory experiments, Berlin and Clark (1998) established that embryos make vocalisations from within the egg 24-28 hours before hatching. These appear to function as signals to attract parental care and attention, since parent birds are able to locate a calling egg,

even among a brood of older nestlings that have already hatched. Having done so, they proceed to help with the hatching process by assisting in the breaking of the shell along the crack in the egg.

Whilst ensuring an egg hatches is clearly in the interest of parents and offspring alike, not all subsequent interactions between the two are necessarily so harmonious. Trivers (1974) introduced the concept of genetic conflict over the allocation of parental investment, suggesting that offspring might be selected to solicit more attention than parents are selected to give. Experiments on the budgerigar (Stamps *et al.*, 1985) indicate that parent-offspring conflict is a feature of this species. For instance, as chicks mature, they are able to make stronger demands for food from their parents when the latter return to the nest with provisions. Recently hatched nestlings can only vocalise and wave their heads when begging for food; six to eight day old chicks can stretch their necks up towards their parents' beaks; and older nestlings are able to run towards their parents, lunge at their beaks and physically displace any nearby younger siblings. The asynchronous manner in which budgerigar clutches hatch means that older chicks have a significant competitive advantage over their younger siblings, and the potential to obtain a disproportionately high share of resources. This is unlikely to be desirable from a parent bird's perspective, unless food is particularly scarce, in which case it may allow its youngest offspring to starve in order to guarantee its siblings enough food to survive.

Stamps *et al.* (1985) found that female budgies appear to have evolved a counter-strategy to oppose their offspring's selfish demands, allocating food primarily on the basis of size (favouring smaller individuals) and devaluing the begging rates of larger

chicks. Although this strategy effectively overrides any advantages larger chicks may have in procuring food, it is temporally costly, since females need time to discriminate between their various offspring, as well as to avoid the begging attempts of their largest chicks. Males, who are generally less responsible for the direct provisioning of offspring (tending to allo-feed their mates, who then transfer food to chicks themselves) do not appear to have evolved this strategy; when they do directly feed their young, they tend to provision those individuals that beg the hardest.

Once they have fledged, budgerigar chicks join their parents' flock (Radke, 1988). The extent to which they continue to associate with their parents and siblings post fledging has not been studied in the wild. In a three-week long study of newly fledged captive budgerigars, however, Stamps *et al.* (1990) found that fledglings initiated more social interactions than expected with their siblings and fathers, and that many formed a mutual affiliative relationship with one of their siblings. Patterns of social activity during these three weeks were comparable for male and female fledglings, and were unrelated to fledging order. Family size, though, did affect young birds' social behaviour, with fledglings from broods of one tending to initiate and receive more social interactions from parents and non-related adults than did fledglings with siblings.

In summary, budgerigars are flock-living, group-foraging, nomadic birds whose movements are determined by the availability of food and water. Foraging in the presence of conspecifics may provide individual budgerigars with the opportunity to learn socially about the location and quality of food patches, and / or (perhaps especially in the case of young birds) about novel food sources. Parent-offspring and

sibling-sibling interactions present interesting possibilities for directed social learning. So, too, does the highly pair-bonded nature of adult budgerigar social interactions. Males and females within a pair spend more time in close proximity, and with fewer displays of agonistic behaviour, than they do with non-partners. This may, for instance, enhance their opportunities for social learning from one another (and reduce their opportunities for social learning from other flock-mates) when foraging together in the non-breeding season. During the breeding season, however, sex differences in behaviour (males forage and return to the nest to provision females incubating eggs in the nest) may restrict possibilities for intra pair bond social learning of foraging information.

Behavioural Studies

Budgerigars have been kept in captivity from the mid 18th Century onwards (Cayley, 1933), and as such are easily obtainable for use in behavioural studies. Moreover, captive budgerigars today exist in a variety of colour morphs (the earliest non-wild-type morph being believed to have arisen around 1870 – Cayley, 1933) – an attribute that can aid with the identification of individual birds during group studies. To date, most interest in the budgerigar's behaviour has revolved around its vocal abilities. An increasing number of studies, however, are beginning to address its capacity for various forms of social learning, ranging from social facilitation to motor imitation. Studies into both of these aspects of budgerigar behaviour are reviewed briefly below.

Vocal Learning

Parrots are unusual among birds in being able to learn new vocalisations throughout life, irrespective of season (Hile *et al*., 2005). Adult budgerigars have a complex vocal repertoire comprising numerous different call types, as well as a long, rambling, non-stereotyped warble song (Brockway, 1964a, 1964b; Farabaugh *et al*., 1992; Farabaugh *et al*., 1994).

The 'distance' or 'contact' call is the most frequently used sound in the budgerigar repertoire (Wyndham, 1980). Females typically produce one or two types of call, whilst males produce in excess of 10 (Faraborough *et al*., 1994). Contact calls are produced repeatedly when a flock or mated pair is in flight or about to fly; when individuals become separated from their flock mates; when mates greet one another after separation; and when birds are preparing for their evening roost (Brockway, 1964a, 1964b; Wyndham, 1980; Farabaugh *et al*., 1994). Since budgerigars live in social groups, contact between, and recognition of, group members is potentially important. Thus, a common contact call may act as a badge of flock membership and facilitate social bonding (Brittan-Powell *et al*., 1997). As budgerigar groups are also highly mobile, calls may additionally aid in the coordination of synchronous movements (Faraborough *et al*., 1994).

The contact call of adult birds, which appears to develop from the food-begging call of young nestling budgerigars, emerging in recognisable form at the time of fledging (Brittan-Powell *et al*., 1997), is thought to play a role in budgerigar mate choice. For instance, experiments on captive birds have demonstrated that females placed in a

dyadic choice chamber preferentially affiliate with males whose initial calls are similar to their own (although in the absence of further evidence regarding which birds females subsequently establish pair-bonds with, and/or the paternity of their offspring, this cannot be considered compelling evidence of mate choice) (Hile *et al*., 2005). Furthermore, once mated, males modify their calls to imitate those of the female more precisely (Hile *et al*., 2000; Striedter *et al*., 2003; Moravec *et al*., 2006). The exact purpose of this is unclear. However, it has been suggested that imitating a female's call may help to cement or continually renew a pair bond (thus reducing paternity uncertainty), and may even manipulate her behaviour or reproductive physiology in such a way as to stimulate ovulation (Striedter *et al*., 2003) – something likely to be beneficial in the dry environments budgerigars inhabit, where females must quickly come into reproductive condition following rain in order to maximise their chances of reproductive success (Wyndham, 1981). Males with pre-pairing calls that are highly similar to those of their prospective mate have been shown to subsequently provide a greater degree of care to their offspring than males with dissimilar pre-pairing calls (Moravec *et al*., 2006). Thus, females may use this as a predictor of paternal investment, although why the two should be correlated is currently unclear.

Social Learning

Being gregarious birds, budgerigars have the opportunity to interact with, and potentially learn from, fellow conspecifics throughout life, and indeed, there is evidence to suggest that they make use of social information in a variety of contexts.

As already noted, budgerigars are social foragers, travelling in flocks from one food patch to another. When entering an unknown habitat with unknown resources, previous studies (not on budgerigars) have shown that an animal's foraging efficiency may be enhanced by paying attention to the activity of others (Brown, 1988; Heyes, 1993; Avery, 1994; Galef and Giraldeau, 2001) – both in order to learn about novel foods (Turner, 1964; Mason and Reidinger, 1981), and to discover where food is located (Krebs *et al*., 1972; Krebs, 1973; Ward and Zahavi, 1973).

Studies of a number of social species have found that observation of foraging conspecifics can promote foraging in unfamiliar situations, such as in the presence of a novel object (e.g., in zebra finches, *Taeniopygia guttata* – Coleman and Mellgren, 1994), or when novel food is presented (e.g., in gerbils, *Meriones unguiculatus* – Forkman, 1991; and capuchin monkeys, *Sapajus apella* – Visalberghi and Fragaszy). Soma and Hasegawa (2004) predicted that budgerigars, too, might habituate more quickly to feeding in the presence of novel objects when exposed to them as part of a group rather than on their own. To test this, they devised a set of experiments in which budgerigars could forage from a bowl positioned next to one of a variety of previously unseen items. In some tests, birds were housed alone, while in others they were housed in groups of six. As predicted, mean latency to feed was significantly lower when birds were maintained socially rather than asocially. This effect was mainly attributable to the fact that once one 'pioneer' individual began to forage, the remaining five birds in its group would typically join it within a short space of time. Soma and Hasegawa (2004) ascribed this to social facilitation, although it is possible that competition for access to the feeder was partly responsible for the earlier onset of feeding activity during social trials.

In what was described at the time as a clear-cut case of motor imitation, Dawson and Foss (1965) reported that five naïve budgerigars, given the opportunity to observe a demonstrator budgerigar use one of three different methods to open a covered food dish, subsequently used the same method to uncover their own food dishes. Two later attempts to replicate this effect (Galef *et al*., 1986; Moore, 1992), however, were less convincing. Moore (1992) failed to find any evidence that observer birds copied the cover-removal methods of their demonstrators, while Galef *et al.* (1986) found that, although observers exhibited a slight tendency to use the same cover-removal methods as their demonstrators, the effect was of brief duration and marginal significance.

Heyes and Saggerson (2002) argued that the 'elusiveness and fragility' of Dawson and Foss's effect could be the result of a lack of imitative ability on the part of budgerigars, but that other explanations could not be ruled out. They suggested, for instance, that the use of flat food covers might elicit strong response tendencies that compete with, and possibly override, the effects of conspecific observation, that use of the foot versus the beak to dislodge a food cover might not be sufficiently discriminable for budgerigar observers, and that using a procedure in which observers are given one demonstration trial and one test trial daily, might not be optimal for detecting imitation.

To re-address the issue, Heyes and Saggerson (2002) ran a two-object/two-action test in which observers were able to watch a conspecific demonstrator repeatedly removing one of two stoppers from the horizontal surface of a food box either by pulling it up or pushing it down. After this, they were given 15 minutes' access to

both stoppers and rewarded with food for all the removal responses they made in this time, irrespective of which stopper they removed and the direction in which they displaced it. Though displaying an overall bias in favour of pushing the stopper downwards, Heyes and Saggerson (2002) found that budgerigars that had observed 'up' responding made significantly more 'up' responses of their own than those that had observed 'down' responding, and vice versa. They concluded from this that budgerigars do, after all, have the capacity to mimic body movements. Hoppitt and Laland (2008), however, subsequently pointed out that these data are generally consistent with an emulation interpretation, since the movement not only of the bird, but of the stopper itself, differed in pull-up and push-down demonstrations. They also pointed out that response facilitation was impossible to rule out, since no control experiment was implemented to determine whether observer birds were inclined to produce the same body movements they had seen a demonstrator make irrespective of context (i.e., not just in the presence, but also in the absence, of the stoppers and food box). Indeed, findings from two recent studies suggest that budgerigars do appear to be subject to response facilitation. Mui *et al.* (2008) found that the sight of another individual's actions tended to elicit the same action from an observer, even when doing so interfered with the efficient performance of a task. Meanwhile, Miller *et al.* (2012) recently provided further evidence of this effect in their study of contagious yawning and stretching in groups of captive budgerigars.

Further experiments involving two-action tests have revealed that budgerigars are responsive to 'virtual' demonstrators (video play-back images of conspecifics) as well as live ones (Mottley and Heyes, 2003). Moreover, their tendency to respond to a two-

action task in the same fashion as their demonstrator can persist for some time (at least 24 hours) (Richards *et al*., 2009).

In summary, current evidence suggests that budgerigars in the company of conspecifics are subject to social facilitation and response facilitation effects. The results from a number of two-object/two-action tests further suggest that naïve budgerigars may be able to imitate (or possibly emulate) the actions (or in the case of emulation, recreate the results of the actions) of knowledgeable conspecifics to obtain a food reward. Though not completely unambiguous, this remains some of the strongest available evidence collected to date of contextual imitation in animals.

This Study

In addition to being a social species with documented social learning abilities, budgerigars offer a number of practical advantages that leave them well suited to studies of social learning in captivity. They are readily obtainable and easy to keep, individually identifiable by plumage, easy to sex, and they exhibit little aggression, enabling birds to be transferred from one group to another with relative ease during experimental manipulations.

Birds and Housing

The budgerigars used during the course of this study were kept in small groups (8-15 individuals) and housed indoors in the University of St Andrews bird facility. Groups were kept in miniature aviary cages in two rooms (two to three cages per room). Exact cage dimensions and group sizes varied according to experiment, and are documented in detail in Chapters Three and Five.

Aviary floors were covered in wood chip pellets, and numerous perches and forms of environmental enrichment were provided. Full time technical staff provided husbandry and the St Andrews University vet monitored the birds on a monthly basis. Water, food (Bucktons© (Driffield, East Yorkshire) Quality Cage and Aviary Food), grit and cuttlebone were freely available. Additional foods were also provided, including eucalyptus, sweetcorn, carrot, apple, broccoli, kale, spinach and cress. Millet spray, a highly desired food item, was provided only during experiments. Rooms were air conditioned at a temperature of 20-22°C and maintained on a light/dark cycle of 12/12 hours. 'Sunset' time in the rooms was staggered by half an hour (1800 hours in one room and 1830 hours in the other) to allow experiments to be run in both rooms on the same day.

A total of 25 adult budgerigars, approximately one to two years old at the beginning of the study, were purchased from local breeders for use in this study. A further 25 late juvenile / young adult budgerigars, bred in the bird unit from our adult stock, and approximately six months of age at the beginning of the study, were also available for use. Each bird was fitted with a Budgerigar Society leg ring for identification, and

groups were assembled in such a way as to ensure birds could be distinguished by their plumage, since rings were not always readily visible.

Birds remained healthy for the duration of the work described in Chapters Three and Four. During the course of the work detailed in Chapter Five, four birds in one group fell ill with air sac mites. This group was excluded from experiments in part two of the study whilst all group members underwent treatment for the condition.

CHAPTER THREE

SCROUNGING AND THE SPREAD OF NOVEL FORAGING BEHAVIOUR THROUGH CAPTIVE BUDGERIGAR GROUPS

Abstract

Foraging in groups can provide the opportunity for the social learning of new skills. At the same time, it can create opportunities for naïve animals to scrounge food produced by competent foragers, potentially reducing the formers' motivation to express and/or learn new skills.

Using five groups of six to eight captive budgerigars, *Melopsittacus undulatus*, I examine the effect of these opposing influences on the spread of novel task solving behaviour. I vary social learning opportunities by inserting task competent 'demonstrator' birds into some groups at the start of trials, and manipulate scrounging opportunities by loading some tasks with large quantities of food and others with small quantities.

I find that, when birds reaped large rewards from scrounging, they were less inclined to solve tasks themselves. Any positive influence demonstrators exerted on the spread of solving behaviour was seemingly largely mitigated by the fact that their 'demonstrations' (task solves) not only provided increased scope for social learning, but also for scrounging. Furthermore, the efficiency with which demonstrators solved multiple tasks restricted the number of unsolved tasks available for remaining group members to access.

Upon removal of a group's demonstrator (typically its most proficient and prolific task solver), however, I find that scroungers were sometimes able to switch to become

task solvers, particularly when scrounging had previously conferred a high level of reward.

Thus, in budgerigars, I find evidence that scrounging suppresses immediate performance of new skills, but that it does not inhibit – in fact, may even facilitate – their underlying learning. When studying the spread of innovations through animal populations, it is important, therefore, to recognise that skill learning may not straightaway translate into skill expression.

Introduction

Group foraging provides animals with opportunities for kleptoparasitism, or 'scrounging'. 'Scroungers' are individuals that exploit resources (often food) that others, termed 'producers', have made available (Barnard and Sibly, 1981; Giraldeau and Caraco, 2000). Scrounging operates in potential conflict with social transmission of new foraging skills, and may be responsible for the failure of some innovations to spread to most or all members of a group, as in captive pigeons, *Columbia livia* (Giraldeau and Lefebvre, 1986; see also Reader and Laland, 2003). To date, producer-scrounger interactions have been studied in captivity among several species of group foraging birds (pigeons – e.g., Giraldeau and Lefebvre, 1986, 1987; zebra finches, *Taeniopygia guttata* – Beauchamp and Kacelnik, 1991; chickens, *Gallus gallus domesticus* – Nicol and Pope, 1994; and ravens, *Corvus corax* – Fritz and Kotrschal, 1999). Here, I examine their role in the uptake of new foraging behaviour in small groups of captive budgerigars, *Melopsittacus undulatus*, for the first time.

The dynamical interaction between producing and scrounging strategies has been investigated using evolutionary game theory (Barnard and Sibly, 1981; Giraldeau and Caraco, 2000). The producer-scrounger 'game' has the potential to generate a type of mixed, flexible evolutionarily stable strategy (ESS) (Maynard Smith, 1974; Dawkins, 1976), since neither strategy is stable when dominant. A population containing only producers will be susceptible to invasion by scroungers seeking to minimise their own resource exploitation costs, whilst in a population containing only scroungers, no individual will receive any payoff at all. Rather than rigidly employing only one strategy, however, as would be the case in a true ESS, individual animals may act as mixed strategists, monitoring the relative profitability of producing versus scrounging, and switching between strategies according to their current payoff (Barnard and Sibly, 1981; Giraldeau and Lefebvre, 1986; Giraldeau and Templeton, 1991; Mottley and Giraldeau, 2000). Indeed, so long as the behaviours involved in producing and scrounging are not completely incompatible (i.e., so long as individuals that search for new food patches to exploit are not completely unable to simultaneously monitor the foraging activities of others in their group), then it is possible that individuals may not only adopt the role of pure producers when foraging under some circumstances, and of pure scroungers when foraging under others, but potentially behave as opportunists, using producing and scrounging foraging strategies interchangeably within a single foraging bout (Vickery *et al.*, 1991). In any given group of animals, the optimal ratio of producers to scroungers is likely to depend on several factors, including the size of the group; whether or not producers gain a monopolisable 'finder's / producer's share' upon being the first to access a food source, and how large this share is in relation to the remainder of the food available (the 'scroungers' share') (Vickery *et al.*, 1991; Giraldeau and Caraco, 2000); and group members' risk of starvation (Caraco and

Giraldeau, 1991). In general, the larger the producer's share, the smaller will be the opportunity for scrounging.

When scroungers reap large rewards, their incentive to display much production related behaviour is likely to be small. However, whether scrounging interferes not only with an animal's performance of new skills, but also its underlying learning of these skills, is contentious. Findings from some studies suggest that scrounging has an inhibitory effect on learning. Nicol and Pope (1994) found that naïve chickens kept in a 'free' condition, in which demonstrators and observers were allowed to freely interact during a task solving exercise, were much less successful at subsequently solving the task, than were observers that had been prevented from interacting with their demonstrator by means of a screen. Similar apparently inhibitory effects of social foraging on individual learning have also been reported in captive pigeons (Giraldeau and Lefebvre, 1987), capuchin monkeys, *Sapajus apella* (Fragaszy and Visalberghi, 1990), and zebra finches (Beauchamp and Kacelnik, 1991).

A number of explanations have been proposed for this inhibitory effect on learning. First, it could be that scrounging provides naïve individuals with feeding opportunities that may keep them from investing the time necessary to acquire whatever skill the producers in the population are using (Giraldeau, 1984). Secondly, scrounging may cause 'blocking' or 'overshadowing' (Shettleworth, 1998). Blocking occurs when an animal has already learned one conditioned stimulus that signals an unconditioned stimulus (such as the location of a producer being a reliable indicator of the location of food), which then reduces its ability to learn that a second conditioned stimulus (such as a coloured lid on top of a jar of food) also signals the unconditioned stimulus.

Overshadowing occurs when two or more conditioned stimuli (such as a producer stationed at a jar of food with a coloured lid on top of it) are presented simultaneously, but one is more salient than the other(s), causing an animal to learn little about the value of the less salient stimulus / stimuli in signalling the unconditioned stimulus.

In certain studies where scrounging has been reported to have a negative effect on skill learning, however (e.g., Giraldeau and Lefebvre, 1987; Nicol and Pope, 1994), other factors may also have been at work. In these studies, when scrounging took place, subjects were able to interact with the other individuals in their group, whereas when scrounging was prevented, individuals were physically separated from the rest of the group. Under 'free' conditions, the close-up presence of other individuals may have obscured the actions of producers from naïve individuals' view and been at least partly responsible for their failure to learn new skills. In the case of Nicol and Pope's (1994) study, a further barrier to skill acquisition by naïve hens in free conditions appeared to be that, in the absence of partitions, demonstrator hens attempted actively to defend the food resources they had produced by threatening the naïve observer hens in their group.

Empirical support for the hypothesis that foraging under free, as opposed to more restricted conditions, may interfere with animals' ability to acquire new skills comes from a study by Giraldeau and Lefebvre (1994), who found that pigeons in the company of a large number of fellow naïve bystanders were slower to learn a tube opening task from a demonstrator than were birds housed with fewer bystanders. Further support is provided by Lefebvre and Helder (1997), who showed that pigeons that scrounged singly from a producer were subsequently able to exhibit producing

behaviour when tested by themselves, but that pigeons that had scrounged as part of a group were not.

Indeed, some studies have found that scrounging from others can aid previously unskilled animals in the learning of new behaviours. Scrounging from an individual engaged in a particular behaviour with a particular object may be important in attracting a naïve animal into close proximity with a skilled 'demonstrator', and grant it the opportunity for social interaction and detailed observation of the actions necessary for successful exploitation of the resource (Caldwell and Whiten, 2003). By providing reinforcement, scrounging may also subsequently increase the tendency of naïve individuals to investigate, and learn how to access food from novel sources, for themselves (Thornton and Malapert, 2009). Even if a scrounger encounters only artefacts left behind by a skilled individual's labour, this may be sufficient to facilitate learning. Two well documented cases in which this may play at least a partial role are that of milk bottle top opening by British tits, *Parus* spp. in the mid-twentieth century (Fisher and Hinde, 1949; Hinde and Fisher, 1951), and pine cone stripping by black rats, *Rattus rattus*, in Israel (Zohar and Terkel, 1991; Aisner and Terkel, 1992; Terkel, 1996). Tits, for instance, are able to acquire bottle opening behaviour following a period of exposure to already-opened bottles, and access to the reward (cream) located inside them (Sherry and Galef, 1984). Pine cone stripping behaviour in black rats is acquired by young rats with pine cone stripping mothers. Mother rats, however, do not directly teach or demonstrate efficient pine cone stripping to their young. Rather, cones partially stripped by an experienced mother have their scales exposed in such a way that a young rat gnawing at a discarded cone can easily remove any remaining scales in an efficient spiral pattern to get at the seeds underneath – something that

naïve rats encountering completely unopened cones are unable to do. Thus, efficient stripping of pine cone scales is learned by young rats following their mother around, stealing partially stripped cones from them, and continuing the stripping themselves (Aisner and Terkel, 1992; Terkel, 1996).

Here, I examined the behaviour of small groups of captive budgerigars when given repeated presentations of four different sets of novel foraging tasks. Each set of foraging tasks consisted of eight identical tasks, allowing multiple opportunities for the set of tasks to be solved within one presentation, potentially by multiple individuals. In each case, a single task solve yielded a portion of seeds, which could be fed on by the task solver and/or any bird that successfully scrounged from it. I varied the size of these portions in order to try and manipulate the proportion of the reward that was obtained by the task solver (the producer's share) in comparison to any reward obtained by non task solvers (the scroungers' share). Assuming that producers would have time to monopolise a roughly constant quantity of seeds following a task solve, before being displaced by other members of their group, I expected the small portions to confer a large producer's share (and a small scroungers' share) in relation to the total amount of food yielded by a task solve, and the large portions to confer a proportionally smaller producer's share (and larger scroungers' share). I predicted that:

1) A greater proportion of group members would solve at least one task when the producer's share was high and the scroungers' share low than in the reverse condition.

2) Having made their first task solve, birds would be more likely thereafter to consistently act as producers / opportunist producer-scroungers (and not revert back to operating as pure scroungers), when the producer's share was high and the scroungers' share low, than in the reverse condition.

I seeded my groups with a pre-trained, task competent 'demonstrator' bird for two of their four series of task presentations. Demonstrators served as 'guaranteed innovators', able to begin solving tasks as soon as they were presented. If social learning, in addition to producer-scrounger dynamics, is important in determining the uptake and spread of new foraging skills through budgerigar groups, I predicted that:

3) Birds would generally be quicker to make their first solve of a particular task when there was a proficient demonstrator in their group than when there was not.
4) However, since demonstrators would not only provide group members with the chance to observe tasks being solved, but potentially also increase their opportunities to scrounge from pre-solved tasks, I expected any positive impact a demonstrator had on its naïve group mates' acquisition of task solving behaviour, to be more marked under conditions where the producer's share was high and the scroungers' share low, than when the producer's share was low and the scroungers' share high.

Lastly, I examined task solving performances of budgerigars following the removal of their group's demonstrator (typically, the group's most prolific producer). I assessed the behaviour of individuals from groups that had lost their demonstrator in relation to

individuals from groups that had not been seeded with a demonstrator, and from which no birds were removed. I also compared the behaviour of individuals from demonstrator-containing groups in which food portions were large (high scroungers' share), with that of those from demonstrator-containing groups in which food portions were small (low scroungers' share). I predicted that:

5) If birds used producer-scrounger strategies opportunistically, individuals in groups that had lost their demonstrator, a prolific producer, should be more likely to increase their production behaviour following its removal, than should individuals in control groups (from which no producer had been removed, and whose group dynamics had not been altered) over the equivalent set of trials.
6) If scrounging repressed performance *and* learning of foraging skills, this compensatory increase should be relatively more marked in groups provided with tasks containing small portions of seeds (low scroungers' share), in which learning and performance ought to have been less strongly inhibited than in groups provided with tasks containing large portions of seeds (high scroungers' share). Conversely, if scrounging repressed performance but enhanced underlying learning of foraging skills, I expected the opposite – namely, that this compensatory increase should be more marked under high scroungers' share conditions than under low scroungers' share conditions.

Methods

Birds and Housing

Experiments took place in the St Andrews University bird unit, and used five groups of mixed-sex, mixed-age, individually identifiable budgerigars. Three groups contained eight birds, two with four adults and four juveniles, and another with seven adults and one juvenile. A fourth group contained seven birds: three adults and four juveniles, and a fifth group contained six birds: three adults and three juveniles. All adult budgerigars were purchased from local breeders and were between one and two years old at the beginning of the experiment. All juveniles were bred in the St Andrews University bird unit, and were approximately six months old at the beginning of the experiment. Each bird was fitted with a Budgerigar Society leg ring for identification. Groups were selected such that the birds could be distinguished by their plumage, since rings were not always readily visible.

Groups were housed indoors in the University of St Andrews birdhouse and kept in two rooms in miniature aviaries of size 70 cm W x 140 cm L x 120 cm H. Rooms were air conditioned at a temperature of 20-22° C and maintained on a light/dark cycle of 12/12 hours. Since birds were most motivated to feed close to the end of each day, 'sunset' time in the rooms was staggered by half an hour (1800 hours in one room and 1830 hours in the other) to allow experiments to be run in both rooms on the same day. For further details of housing conditions, see Chapter Two.

Design

Over a period of three months, groups were presented with four different types of foraging task, the Tube, Flap, Lucky Dip and Drawers tasks (Fig. 3.1). During a trial, eight replicates of each task type were presented, in two rows of four, on one half of a group's aviary floor (Fig. 3.2). Each task could be solved in order to yield a highly valued food type, millet seed. Groups were presented with two task types stocked with a large portion of seeds (four clusters) inside each task (low producer's share/high scroungers' share – hereafter, 'high-scrounge condition'), and two stocked with a small portion (one cluster) per task (high producer's share/low scroungers' share – hereafter, 'low-scrounge condition'). Two task types were presented after groups had been seeded with a demonstrator bird that was already competent at accessing food from that particular task, and two were presented in the absence of a demonstrator (Table 3.1). (Note that no 'sham' demonstrator (naïve bird) was inserted into groups in non-demonstrated conditions to control for the alteration demonstrators caused in group size / competition for access to tasks when inserted into groups – a limitation in experimental design that is dealt with in the discussion.)

Figure 3.1: From left to right, foraging tasks in pre-training, unsolved and solved state. (i) Tube, (ii) Flap, (iii) Lucky Dip and (iv) Drawers task.

Figure 3.2: Task set-up on the aviary floor (Flap task pictured).

Table 3.1: Task presentations across groups. Condition: ND = Non-Demonstrated, D = Demonstrated; HS = High Scrounge Condition; LS = Low Scrounge Condition. Day: Days (since beginning of trials) on which task was presented. Demonstrator: Group of origin of demonstrator.

Task	Presentation	Group 1	Group 2	Group 3	Group 4	Group 5
Tube	*Condition*	D, HS	ND, HS	ND, LS	D, LS	ND, HS
	Day	1-10	1-10	11-20	21-30	11-20
	Demonstrator	Pool			G2	
Flap	*Condition*	ND, LS	D, LS	D, HS	ND, HS	D, LS
	Day	31-40	21-30	41-50	41-50	31-40
	Demonstrator		Pool	G2		Pool
Lucky Dip	*Condition*	D, LS	D, HS	ND, HS	ND, LS	ND, LS
	Day	81-90	81-90	71-80	61-70	71-80
	Demonstrator	G4	G4			
Drawers	*Condition*	ND, HS	ND, LS	D, LS	D, HS	D, HS
	Day	101-110	111-120	121-130	121-130	101-110
	Demonstrator			G5	G1	Pool

Pre-training

Prior to the experimental presentation of each foraging task, groups were given a period of pre-training to habituate birds to task objects. This involved exposure to four reduced versions of each task, which did not require solving in order for food to be accessed. Pre-training began at least six days before actual test sessions commenced, and ended three days before they commenced, during which time demonstrators were added to some groups. Pre-training was run until all birds in the group had been observed feeding from a reduced task on at least one occasion, and for a minimum of three 60 minute sessions beginning at 1600 hours (Room 1) or 1630 hours (Room 2). Pilot studies from an earlier experiment (Hoppitt *et al.*, manuscript in preparation) suggested this was necessary for birds to be likely to solve the tasks within a feasible time frame.

Demonstrators

In order to allow them time to adjust to their new surroundings, I introduced demonstrators to groups (after the group had been pre-trained) at least three days before the start of trials. Experiments only began once the demonstrator had adjusted to the group (was not the target, or perpetrator, of raised levels of aggression from, or towards, its new group mates). When a demonstrator was transferred to a cage, it was closely monitored for the first few hours following translocation. In most cases, demonstrators experienced some very mild aggression (in the form of displacement from perches) from other individuals in the period immediately following their transfer. These interactions, however, usually all-but ceased within one hour. Had agonistic behaviour been sustained, or had the demonstrator or another bird appeared

to be in danger of injury, the demonstrator would have been removed, returned to its original group, and replaced with another task-competent bird. Fortunately, it was never necessary to do this.

To minimise individual stress, no bird was used as a demonstrator more than once. Demonstrators came either from a 'pool' of 13 one-year-old birds that were not part of any of the experimental groups, or from groups that had already been presented with a particular task, and which contained individuals that had learnt how to solve tasks and consistently expressed solving behaviour during trials. Birds in the pool were trained to become solvers by exposure to a period of pre-training followed by presentation of some progressively more complete forms of each task. Four pre-training versions of a given task were presented once a day over three consecutive days for one hour at a time. Following this, two intermediate forms, and finally the complete form of the task were presented. Again, each of these forms was presented once a day for three one hour sessions. By the end of this training period, several (two to four) members of the group had typically become competent task solvers.

After seven trials, demonstrators were permanently removed from their experimental group and returned to their original group.

Tasks

i. Tube Task

This comprised a transparent cylindrical plastic tube (13cm L x 3.5 cm diameter), closed at one end and open at the other, taped to a white cardboard base (17 cm L x 8

cm W) for stability. A 15 cm section of millet spray stripped of seeds except at one end (where, depending on experimental condition either one or four clumps of seeds remained), was inserted into the tube such that the seeds were positioned inside it, towards the solid end of the tube, and the seedless section of spray protruded two centimetres from the front of the open end of the tube. To access the seeds at its far end, a bird had to pull the stick of millet out of the tube using its beak, feet, or some combination of the two.

During pre-training, I presented tasks that were empty inside, but with five loose clusters of millet scattered around the outside of the open end of each tube.

ii. Flap Task

This was made from a transparent glass jar (5 cm H x 4.5 cm diameter), covered at the top with a circular piece of white translucent crêpe paper (5 cm diameter) affixed with a small blob of white tack. Millet was taped at the bottom of the jar. To access it, birds had to pull the paper lid off using their beak, push it downwards with their head or a foot, or insert their head underneath the lid.

The pre-training version of the task involved no lid; birds simply had to reach into uncovered jars, into which five millet seed clusters had been placed.

iii. Lucky Dip Task

This consisted of a miniature brown plastic flower pot (4 cm H x 5 cm diameter) stuck to the centre of a 10 x 10 cm white cardboard base. Short sections of millet spray (approximately 2.5 cm in length) were secured inside each pot by pushing their woody stalks into a false floor (clear plastic sheet with small hole punched in the middle taped 1 cm from the base of the pot). The seed clump(s) protruding above the false floor (but below the top of the flower pot itself) were then covered with small (5 x 5 x 5 cm) cubes of pink-coloured artificial sponge until these were level with the rim of the pot. To expose and obtain the underlying seeds, a bird had to displace the sponge pieces using its beak, feet, or some combination of the two.

During pre-training, I presented the flower pots without any sponge, and loaded each flower pot with five clusters of readily accessible millet.

iv. Drawers Task

This was made of a transparent glass jar, open at one end and closed at the other (5 cm H x 4.5 cm diameter), taped on its side to an upturned miniature brown plastic pot (4 cm H x 5 cm diameter), which was in turn taped to a 10 x 10 cm white cardboard base. Inserted into the open end of the jar was a 'drawer' made from a 4.5 cm L x 6 cm W transparent acetate sheet, curved around and stuck to the half-base of a transparent plastic cup (2 cm deep x 4 cm diameter), which formed the front of the drawer. Millet seeds attached to a short section of spray were taped down inside the

drawer. To access these, budgerigars had to remove the drawer from the glass jar, by grasping and pulling it outwards using either their beak or a foot.

During pre-training, I presented the tasks without their drawers in, and with five clusters of millet positioned towards the back of each glass jar.

Experimental Procedure

Groups were presented with tasks in the sequence Tube, Flap, Lucky Dip, and Drawers. Each task type was presented a total of 10 times, once a day at 1700 hours (Room 1) or 1730 hours (Room 2), over 10 consecutive days. Food was removed from birds' cages one hour prior to the beginning of each trial (water remained available throughout). After this time, I ushered the budgerigars into one half of their enclosure, retained them on this side using an opaque white wooden divider inserted through the cage from front to back, and arranged food filled tasks on the floor of the empty half of the cage as previously described. A Canon HG10 high definition video camera was positioned in front of the cage and set to record, the dividing board was removed, and birds were free to interact with the tasks for the next 15 minutes. At the end of this time, tasks were removed from the cage and food was returned, giving the birds 45 minutes in which to feed before room lights went out. Groups were given a resting period of at least 10 days between the final presentation of one set of tasks and the first presentation of the next.

Video Analysis

Videos were watched back using Windows Media Player. During playback, every task contact, task solve, post-solve feed, and task scrounge made by every individual in the group (including the demonstrator, if present) was recorded in Microsoft Excel. The time and duration of each event was also logged. Video analysis was conducted for the full 15 minutes of each trial or until all tasks had been solved and all producers / scroungers had departed from the vicinity.

Task contact: an individual orientated towards and touching or manipulating any part of a task (excluding the cardboard base, if present) with its beak or foot, but failing to solve (access food from) it. Instances of a bird perching on a task to take-off from the floor, landing on a task following flight, or brushing past a task with the body or tail when moving about on the aviary floor, were not counted as contacts.

Task solve: an individual using its beak or foot to manipulate a task in such a way as to yield food from it. Instances of birds yielding food from a task inadvertently (knocking it over after landing on it or brushing past it when moving about on the aviary floor) were (a) very rare and (b) not counted as solves.

Post-solve feed: an individual feeding from a task that it has solved. Feeding defined as per Brockway, 1964a ('the head is held close to food and directed at it. The beak need not necessarily be in contact with the food. The pattern 'feeding' ends when the bird looks up, changes location or interacts with others').

Task scrounge: an individual feeding from a task that has (a) previously been solved by another bird, or (b) from which food is available due to the task having been knocked over.

Analyses

All analyses were carried out in R version 2.13.1 (R Development Core Team, 2011). Demonstrator activity was assessed using two-sided Wilcoxon rank-sum tests. Birds' feeding durations and the division of task solving 'labour' amongst group members were analysed with Linear Mixed Models (*LMMs*) using the nlme package (Pinheiro *et al.*, 2011). Number of task solvers per group were analysed with Generalised Linear Mixed Models (*GLMMs*) using the lme4 package (Bates *et al.*, 2011). (*LMMs* were used when the dependent variable in question was continuous, as in the case of birds' feeding durations; *GLMMs* were used when the dependent variable was binomial, as in the case of individual birds solving / not solving a particular task). Birds' time to first exhibit task solving activity were assessed with a Cox Proportional Hazards Model using the survival package (Therneau and Lumley, 2011). Changes in birds' solving activity were assessed using randomisation tests.

Demonstrator Activity

To examine the extent to which demonstrators, when present in groups, engaged in production activity (i.e., demonstrated task solving to naïve members of their group), and whether or not their activity was significantly different under high-scrounge versus low-scrounge test conditions, I ran four Wilcoxon rank-sum tests. The first of

these compared the total number of task solves performed over the course of trials 1-7 by each of the five demonstrators used in high-scrounge tests, with the total number of task solves performed by each of the five demonstrators used in low-scrounge tests. The second two Wilcoxon rank-sum tests compared the number of trials in which demonstrators performed (a) at least one task solve, and (b) four or more task solves, under high-scrounge versus low-scrounge conditions. The fourth test compared the mean time demonstrators spent feeding after solving a task under high-scrounge and low-scrounge conditions.

Time Spent Foraging (Trials 1-7)

I used a *LMM* to assess birds' mean time (seconds) spent feeding in an average trial under high-scrounge / low-scrounge conditions and demonstrated / non-demonstrated conditions, depending on their 'foraging strategy'. In any given trial, a bird's foraging strategy was defined as 'producer', 'scrounger', or 'opportunist.' Producers fed only at tasks that they had solved; scroungers fed only at tasks other birds had solved; and opportunists fed both at tasks they themselves had solved, and at tasks other birds had solved. Scrounge condition (high / low), demonstrator condition (demonstrated / non-demonstrated) and foraging strategy (producer / opportunist / scrounger) were included in the model as fixed effects, with all possible combinations of two-way interactions (scrounge condition and demonstrator condition; scrounge condition and foraging strategy; and demonstrator condition and foraging strategy) taken into consideration. Potential differences in the difficulty of the four tasks presented were controlled for by including 'task type' as a further fixed effect. 'Group' and 'bird' were added to the model as nested random effects.

I used a second set of *LMMs* to ascertain whether birds' strategy-dependent feeding durations altered as trials progressed, running one *LMM* for each combination of scrounge and demonstrator conditions. Foraging strategy was included in each model as a fixed effect and trial as a covariate, plus the interaction between them. Task type was included as an additional fixed effect, and group and bird were treated as nested random effects.

In all cases, feeding duration data were converted to a normal distribution by log transformation. Homogeneity of variance was checked by examining plots of standardised residuals versus fitted values, and a qq plot was used to check for approximate normality. Here, back-transformed effect sizes and confidence intervals are reported on the multiplicative scale.

Production Behaviour (Trials 1-7)

To analyse whether the number of birds in a group that solved / did not solve a task on at least one occasion over the course of trials 1-7, differed according to scrounge condition (high / low) and demonstrator condition (demonstrated / non-demonstrated), I used *GLMMs* with a binomial error distribution and logit link function. Data were checked for overdispersion prior to running the model. Demonstrators themselves were excluded from the analysis. Scrounge condition and demonstrator condition were included as interacting fixed effects. Task was added as another fixed effect to allow for differences in task difficulty, and group and bird were treated as nested random effects. Effect sizes and confidence intervals are reported on the back-transformed odds ratio scale.

I also ran a Cox Proportional Hazards Model to assess birds' time to first acquire task solving behaviour under different conditions. Scrounge condition (high / low) and demonstrator condition (demonstrated / non-demonstrated), along with task, were included in the model as interacting fixed effects; bird was included as a frailty (random) effect. A censoring indicator was applied to the model to take account of any birds that failed to solve tasks within the timeframe of trials 1-7. Effect sizes and confidence intervals are reported on the back-transformed multiplicative scale.

In addition, for every task presentation in which more than one 'competent' bird was present, I assessed how evenly distributed (or more precisely, how unevenly distributed) task solving performances were amongst skilled group members under different conditions. First, I noted how many members of a group were competent task solvers (had made at least one solve during previous trials) at the beginning of each trial. I then calculated what proportion of solves each of these birds could be expected to perform in that trial, assuming they all played an equal role in performing solves – for instance, if a group contained four task competent birds, each might be expected to account for 0.25 of the total number of solves made during that trial. I then noted how solves had actually been distributed. (Inevitably, when a new group-member made a solve for the first time during a trial, solving distribution for that trial could never quite conform to the expected even distribution, even supposing the already competent members of the group shared most remaining task solves relatively evenly amongst themselves. However, since I re-calculated my predicted even distribution at the start of each new trial – specifically to take into account any additional birds that may have emerged as task solvers during the preceding trial – this is unlikely to have much bearing on my overall results.) Having obtained

expected, and actual, task solving proportions for a given bird in a given trial, I subtracted the former from the latter, and squared the result, to generate a 'deviation score' for that bird. Individual birds' scores were then summed to produce a group deviation score for every trial. When task solves had been shared relatively equally among competent group members during a trial, this number was close to zero. When solving distribution had been more skewed, it was higher. Using these group deviation scores, I ran a *LMM*, converting deviation scores to a normal distribution by log transformation (homogeneity of variance was checked by examining plots of standardised residuals versus fitted values, and a qq plot was used to check for approximate normality), and taking scrounge condition (high / low) and demonstrator condition (demonstrated / non-demonstrated) as interacting fixed effects, task as another fixed effect, and group as a random effect, to determine whether birds' task-solving distributions varied under different scrounge and demonstrator conditions. Back-transformed effect sizes and confidence intervals are reported on the multiplicative scale.

Production Behaviour (Trials 1-10)

I used a *GLMM* with a binomial error distribution and logit link function to assess whether the proportion of birds that performed at least one task solve over the course of trials 1-10 differed according to scrounge condition (high / low) and demonstrator condition (demonstrated / non-demonstrated). Data were checked for overdispersion prior to running the model. Scrounge and demonstrator condition were included in the model as interacting fixed effects. Task was added as another fixed effect, and group and bird were treated as nested random effects. Effect sizes and confidence intervals

are reported on the back-transformed odds ratio scale. (Note that I attempted to run a similar *GLMM* using data from trials 8-10 only, to assess whether the proportion of hitherto non task solving birds that subsequently performed at least one task solve in or after trial eight, differed according to scrounge and demonstrator condition. However, since only a small number of new solvers emerged in this period, there were insufficient data for this model to be fitted).

I also assessed birds' task solving activity in trials 8-10 compared with that in trials 1-7 (post-demonstrator removal versus pre-demonstrator removal). I calculated what overall proportion of task solves each bird accounted for in the first and second 'set' of trials, and subtracted its score in trials 1-7 from its score in trials 8-10, to gauge whether its solving activity had increased, decreased or remained constant. Due in part to a large number of zero scores attributable to birds that failed to solve any tasks in either trial phase, my resultant data were not normally distributed, nor possible to transform to be so. Therefore, I used randomisation tests (Manley, 2006) to generate a null distribution. The test statistic used was the relevant *F* statistic from a *LMM* with group as a random effect, and scrounge condition (high / low) and demonstrator condition (demonstrated / non-demonstrated) as fixed effects. I generated the null distribution for the fixed effects interaction by randomising the order of conditions within each group, and calculating the *F* statistic in each case. I calculated the null distribution for demonstrator condition by randomising the order of demonstrator condition within each group whilst keeping scrounge condition fixed, and vice versa for scrounge condition. In all cases I ran 100,000 randomisations and calculated 95% confidence intervals on the *p*-values.

Results

Demonstrator Activity

Demonstrators were the first members of their group to solve tasks in 3/5 of the high-scrounge, and 4/5 of the low-scrounge test conditions in which they were present, and second in the remaining two high-scrounge and one low-scrounge tests. They were the most prolific producer in their group in 3/5 high-scrounge, and 5/5 low-scrounge tests, and the second-most prolific producer in the remaining two high-scrounge tests.

During the seven trials in which they were present in groups, demonstrators could perform a potential maximum of 56 task solves, since eight tasks were presented to each group in a single trial. Under high-scrounge conditions, the mean total number of task-solves performed by demonstrators was 19.4 (SE ± 7.74). Under low-scrounge conditions, the mean total number of task-solves performed by demonstrators was 30 (SE ± 5.09). A two-sided Wilcoxon rank-sum test revealed no significant difference in the total number of task solves performed by demonstrators under high-scrounge conditions versus low-scrounge conditions (W = 7, p = 0.29, 95% CI = [-34.00, 14.00]).

Furthermore, demonstrators in both condition solved tasks with reasonable consistency, each bird typically performing several task solves per trial (Fig. 3.3). The number of trials in which demonstrators performed at least one task solve did not differ significantly between high-scrounge and low-scrounge conditions (W = 11, p = 0.83, 95% CI = [-4.00, 2.00]). Under high-scrounge conditions, the mean number of

trials in which demonstrators performed at least one task-solve was 4.2 (SE ± 1.16), and under low-scrounge conditions, the mean proportion of trials in which demonstrators performed at least one task solve was 5.0 (SE ± 0.55). Indeed, there was also no significant difference in the proportion of trials in which demonstrators accounted for at least four task solves (i.e., half or more of all available tasks in a given trial) in high-scrounge compared to low-scrounge conditions (W = 13.5, p = 0.92, 95% CI = [-2.00, 4.00]). Under high-scrounge conditions, the mean proportion of trials in which demonstrators performed four or more task solves was 2.6 (SE ± 1.17), and under low-scrounge conditions, the mean proportion of trials in which demonstrators performed four or more task solves was 2.2 (SE ± 0.49).

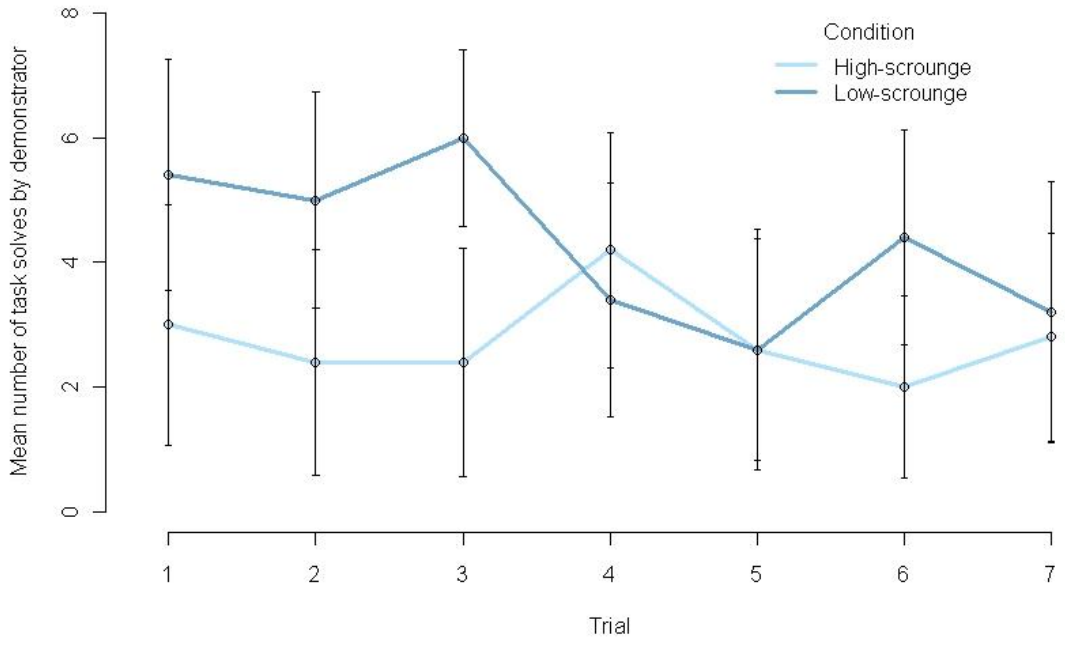


Figure 3.3: Mean number of tasks solved by demonstrators under high-scrounge and low-scrounge conditions in trials 1-7.

Demonstrators under high-scrounge conditions tended to feed for longer from each task that they solved than did demonstrators under low-scrounge conditions (W = 23, p = 0.032, 95% CI = [2.56, 35.82]). Under high-scrounge conditions, the mean number of seconds a demonstrator spent feeding was 35 (SE ±5.82), compared to 17 (SE ±2.94) under low-scrounge conditions. Note that in both conditions, although demonstrators usually stopped to feed for a considerable period of time (at least ten seconds) at a task once they had solved it, they sometimes fed for only a very short amount of time (less than five seconds) before proceeding onto the next task – often because they were displaced from their position at the task by other members of their group. Under high-scrounge conditions, the mean number of tasks per trial that a demonstrator fed at for at least five seconds was 4.20 (SE ±0.50), while the mean number of task per trial at which it fed for less than five seconds was 0.43 (SE ±0.16). Under low-scrounge conditions, the mean number of tasks per trial that a demonstrator fed at for at least five seconds was 4.83 (SE ±0.40), while the mean number of task per trial at which it fed for less than five seconds was 1.12 (SE ±0.26).

In summary, demonstrators *did* demonstrate to a similar extent in both high-scrounge and low-scrounge tests, generally solving numerous tasks, over a number of trials, to provide naïve members of their group with potential social learning and/or scrounging opportunities, although their time spent feeding from tasks once they had solved them differed according to scrounge condition.

Time Spent Foraging (Trials 1-7)

In the *LMM*, two-way interactions between demonstrator condition and scrounge condition, and demonstrator condition and foraging strategy were not significant (respectively, t = 1.00, df = 336, p = 0.32, 95% CI = [0.79, 2.10], and t = -0.023, df = 336, p = 0.91, 95% CI = [0.71, 1.40]). I therefore re-ran the model with these non-significant interaction terms removed.

In the reduced model, there was a significant interaction between scrounge condition and foraging strategy (t = 3.49, df = 338, p = 0.0006) in the time birds spent feeding. In comparison to scrounging, producing – or adopting an opportunistic strategy – was relatively more 'profitable' (i.e., resulted in relatively longer feeding durations) under low-scrounge conditions than under high-scrounge conditions. In high-scrounge conditions, producers spent 2.02x (95% CI = [1.30, 3.16]), and opportunists spent 2.77x (95% CI = [1.88, 4.07]) longer feeding than scroungers. In low-scrounge conditions, however, producers spent 6.55x (95% CI = [3.82, 11.22]), and opportunists spent 3.74x (95% CI = [2.56, 5.49]) longer feeding than scroungers. The ratio of the effect between producers and scroungers was estimated at 3.24x (95% CI = [1.63, 6.37]) higher in the low-scrounge condition than in the high-scrounge condition. The ratio of the effect between opportunists and scroungers was estimated at 1.35x (95% CI = [0.81, 2.25]) higher in the low-scrounge condition than in the high-scrounge condition. Differences in the feeding durations of producers and opportunists were relatively small under both high- and low-scrounge conditions. Opportunists spent 1.36x (85% CI = [0.79, 2.35]) longer feeding than producers under high-scrounge conditions, and 0.58x (95% CI = [0.34, 1.01]) longer feeding than

producers under low-scrounge conditions. The ratio of the effect between opportunists and producers was estimated at 0.43x (95% CI = [0.20, 0.90]) as great in the high-scrounge condition as in the low-scrounge condition (Fig. 3.4).

There was little evidence of an effect of a trained demonstrator on the time birds spent feeding (t = -0.36, df = 338, p = 0.72), with birds under demonstrated conditions feeding for only 1.04x (95% CI = [0.73, 1.24]) longer than birds under non-demonstrated conditions.

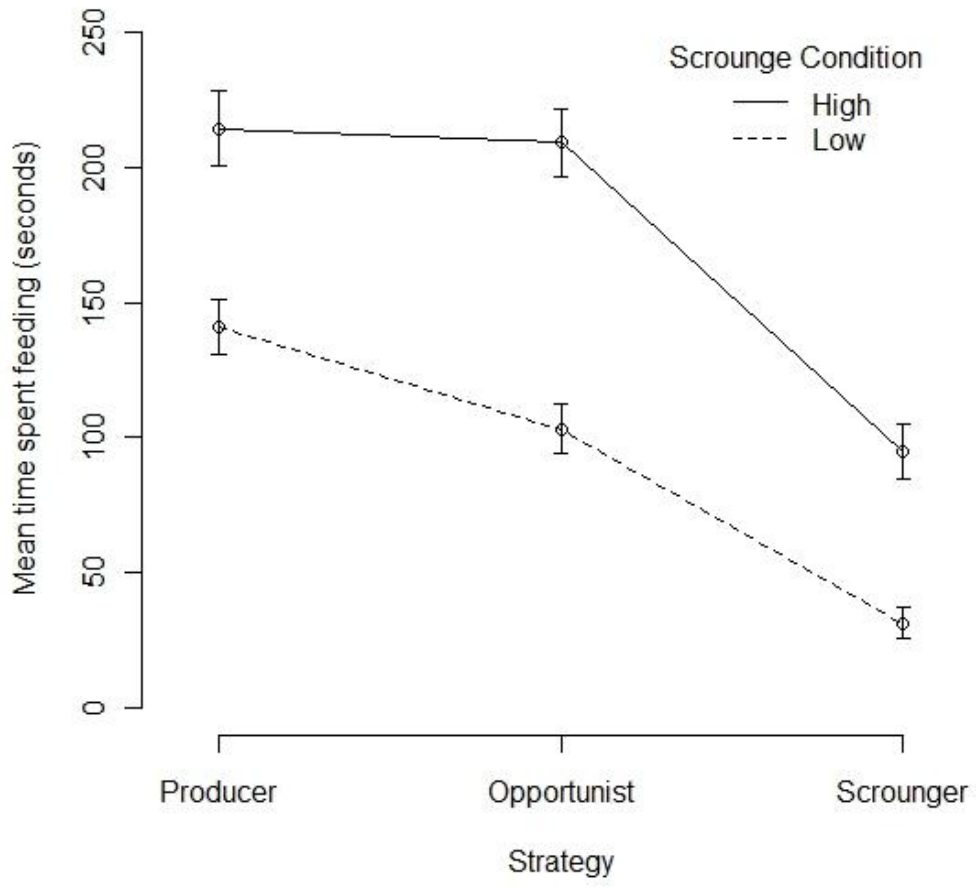


Figure 3.4: Feeding durations per trial according to scrounge condition and foraging strategy (mean ± SE).

In general, differences in the feeding durations of producers and opportunists in comparison to scroungers showed no consistent increases or decreases over the course of trials 1-7 (Fig. 3.5). Two-way interactions between trial and foraging strategy only reached significance under non-demonstrated, high-scrounge conditions (t = 2.52, df = 39, p = 0.016), where the feeding duration of producers in relation to scroungers became 0.51x (95% CI = [0.33, 0.78]) as great, and of opportunists in relation to scroungers became 0.55x (95% CI = [0.37, 0.82]) as great (i.e., showed signs of convergence) with each passing trial. Under other conditions, two-way interactions were respectively: t = 0.30, df = 113, p = 0.77 (95% CI = [0.92, 1.12]) (demonstrated, high-scrounge conditions); t = 0.34, df = 67, p = 0.73 (95% CI = [0.91, 1.13]) (demonstrated, low-scrounge conditions); and t = 1.46, df = 40, p = 0.15 (95% CI = [1.06, 1.58]) (non-demonstrated, low-scrounge conditions).

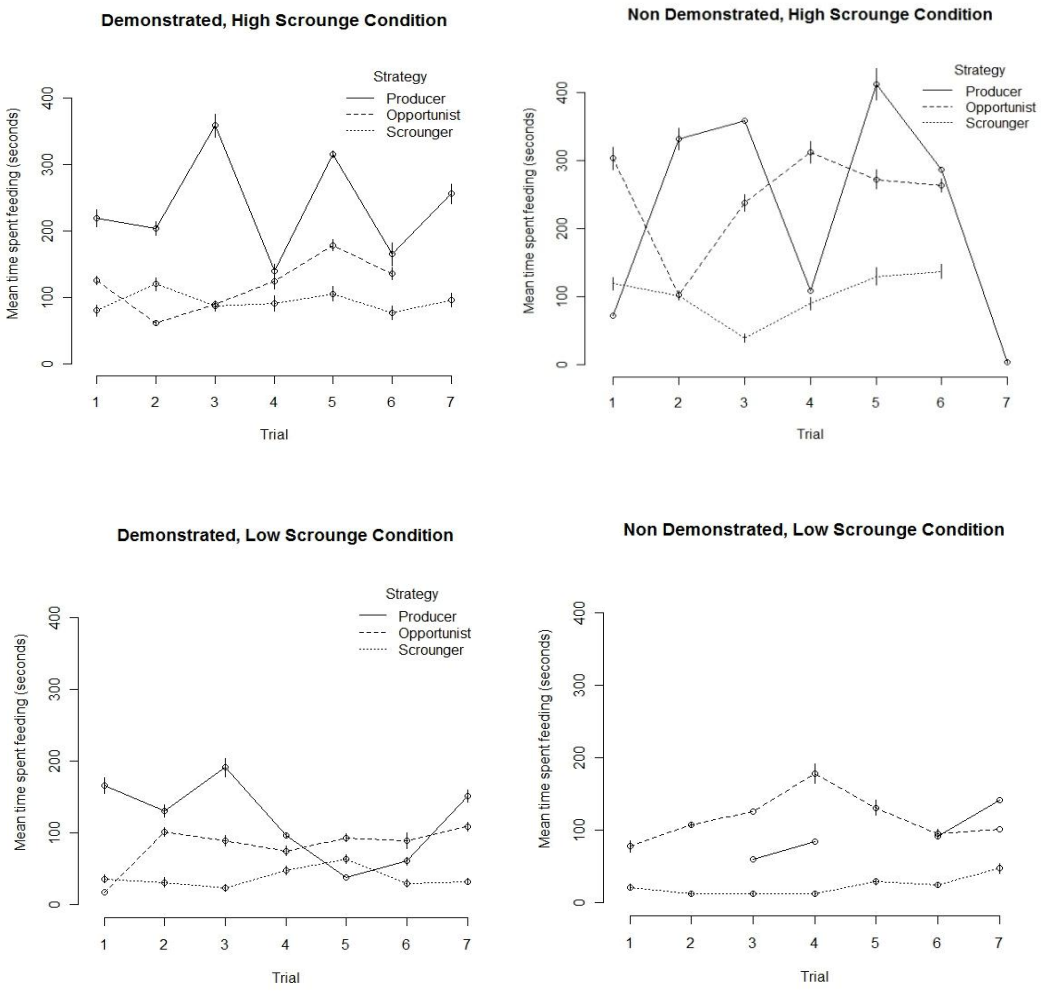


Figure 3.5: Mean feeding durations of producers, opportunists and scroungers over trials 1-7 according to scrounge condition and demonstrator condition (mean ± SE). (Note that among all groups, only one bird acted as a producer in trial 7 of the non-demonstrated, high-scrounge condition, making scrounging opportunities virtually non-existent. In the non-demonstrated, low-scrounge condition, no birds acted as pure producers in trials 1, 2 or 5.)

Production Behaviour (Trials 1-7)

Under all conditions, a greater number of birds tended to act as scroungers than as producers or opportunist producer-scroungers. This difference in numbers was most marked, however, under demonstrated, high-scrounge conditions; and least marked

under non-demonstrated, low-scrounge conditions. There was little difference in the number of birds acting as producers versus as opportunists, although marginally more birds tended to act as opportunists rather than as producers. This was most marked under non-demonstrated, low-scrounge conditions; and least marked under demonstrated, high-scrounge conditions (Fig. 3.10). Notably, demonstrators, when present in groups, exhibited more pure production behaviour than did other task solvers in their group. In demonstrated, high-scrounge trials, demonstrators accounted for 54% of producer activity, and only 3% of opportunist activity; whilst in demonstrated, low-scrounge trials, demonstrators accounted for 79% of producer activity and 34% of opportunist activity.

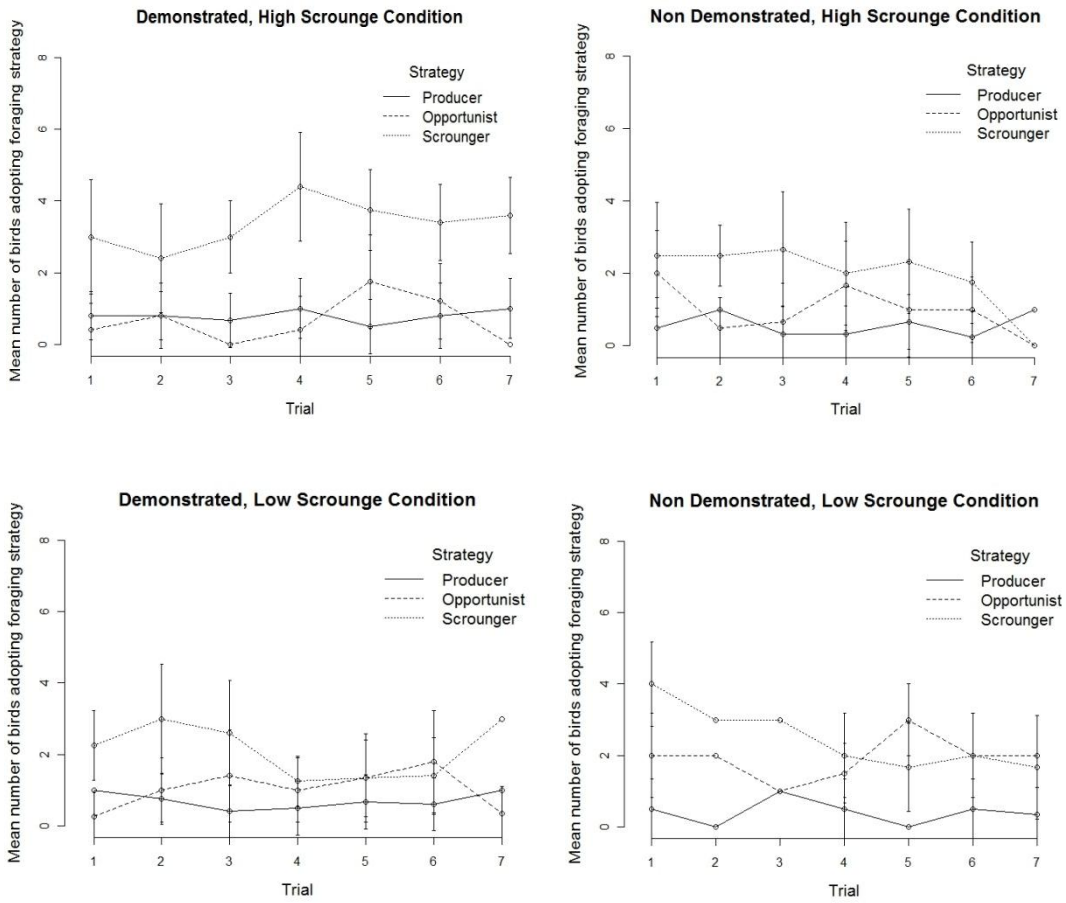


Figure 3.10: Number of producers, opportunists and scroungers per group over trials 1-7 according to scrounge condition and demonstrator condition (mean ± SE).

A *GLMM* revealed no significant interaction between scrounge and demonstrator condition (Wald test: $z = 0.77$, $p = 0.20$, 95% CI odds ratio = [0.59, 12.06]) in the number of task solvers (producers and opportunists combined) that emerged in each group over trials 1-7. Re-running the model with the interaction term removed, I also found no significant difference between scrounge conditions in the proportion of birds that performed at least one task solve (Wald test: $z = -0.10$, $p = 0.92$), with the odds of solving estimated to be only 1.04x (95% CI = [0.50, 2.16]) higher in the low-scrounge condition than the high-scrounge condition (Fig. 3.6). Likewise, there was no significant difference between demonstrator conditions in the proportion of birds that performed at least one task solve (Wald test: z = -0.21, $p = 0.84$), with the odds of solving estimated to be only 1.08x (95% CI = [0.52, 2.25]) higher in the non-demonstrated condition than in the demonstrated condition (Fig. 3.7).

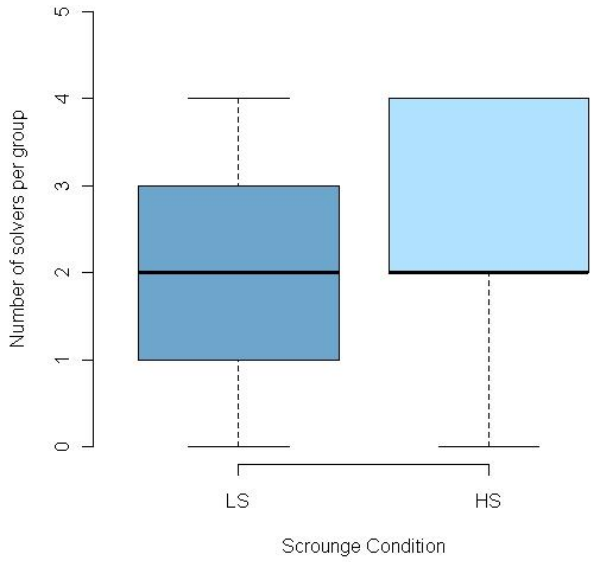


Figure 3.6: Number of task solvers per group (trials 1-7) under low-scrounge (LS) and high-scrounge (HS) conditions. (Bars denote the median number of solvers; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

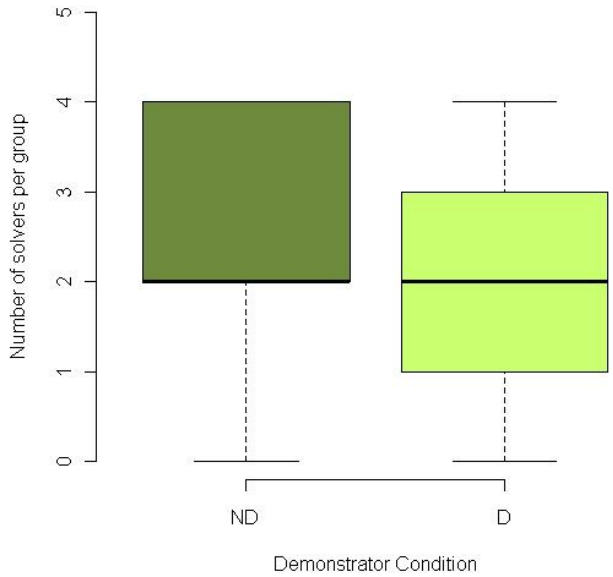


Figure 3.7: Number of task solvers per group (trials 1-7) under non-demonstrated (ND) and demonstrated (D) conditions. (Bars denote the median number of solvers; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

A Cox Proportional Hazards Model showed no significant interaction between scrounge and demonstrator condition (Wald test: $\chi^2 = 0.23$, df = 1, $p = 0.63$, 95% CI = [0.40, 4.47]) in the time taken by birds to make their first task solve. Upon removing the interaction term, there was no evidence of a significant difference in time to first solve between scrounge conditions (Wald test: $\chi^2 < 0.01$, df = 1, $p = 0.99$), with birds making their first task solve only 1.01x (95% CI = [0.55, 1.82]) quicker in low-scrounge conditions than in high-scrounge conditions (Fig. 3.8). There was also no evidence of a significant difference in time to first solve between demonstrator conditions (Wald test: $\chi^2 = 0.03$, df = 1 $p = 0.87$), with birds typically being only 1.05x (95% CI = [0.57, 1.94]) quicker to make their first task solve under demonstrated conditions than under non-demonstrated conditions (Fig. 3.9).

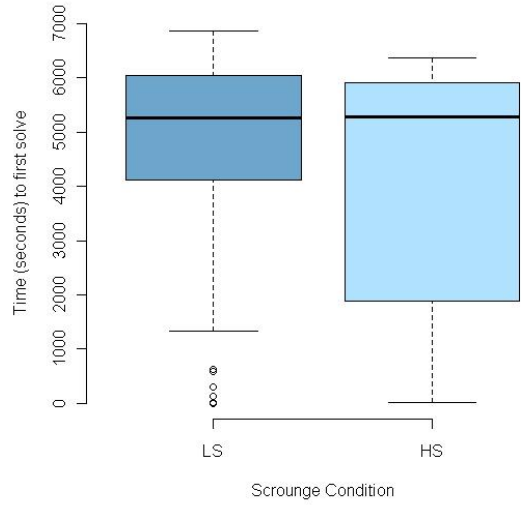


Figure 3.8: Birds' time to first solve tasks (trials 1-7) under low-scrounge (LS) and high-scrounge (HS) conditions. For the purposes of graphical representation, birds that failed to solve tasks within seven 15 minute trials are here assigned a ceiling value 'solve time' of 6300 seconds. (Bars denote the median time to first solve; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

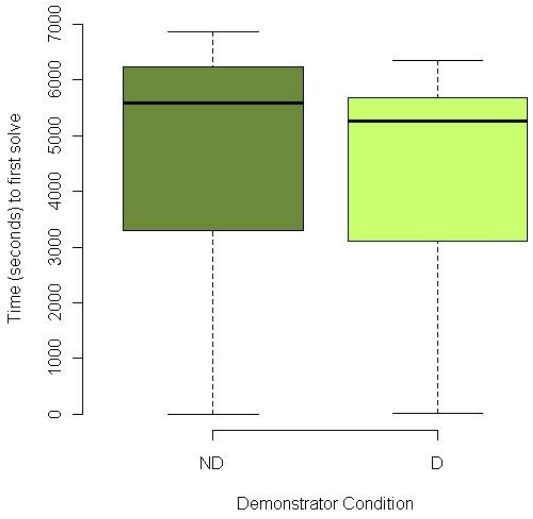


Figure 3.9: Birds' time to first solve tasks (trials 1-7) under non-demonstrated (ND) and demonstrated (D) conditions. For the purposes of graphical representation, birds that failed to solve tasks within seven 15 minute trials are here assigned a ceiling value 'solve time' of 6300 seconds. (Bars denote the median time to first solve; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

Overall, the number of birds in a group that acted as task solvers at least once during a trial was somewhat higher under non-demonstrated, low-scrounge conditions than under any other combination of conditions (Fig. 3.11).

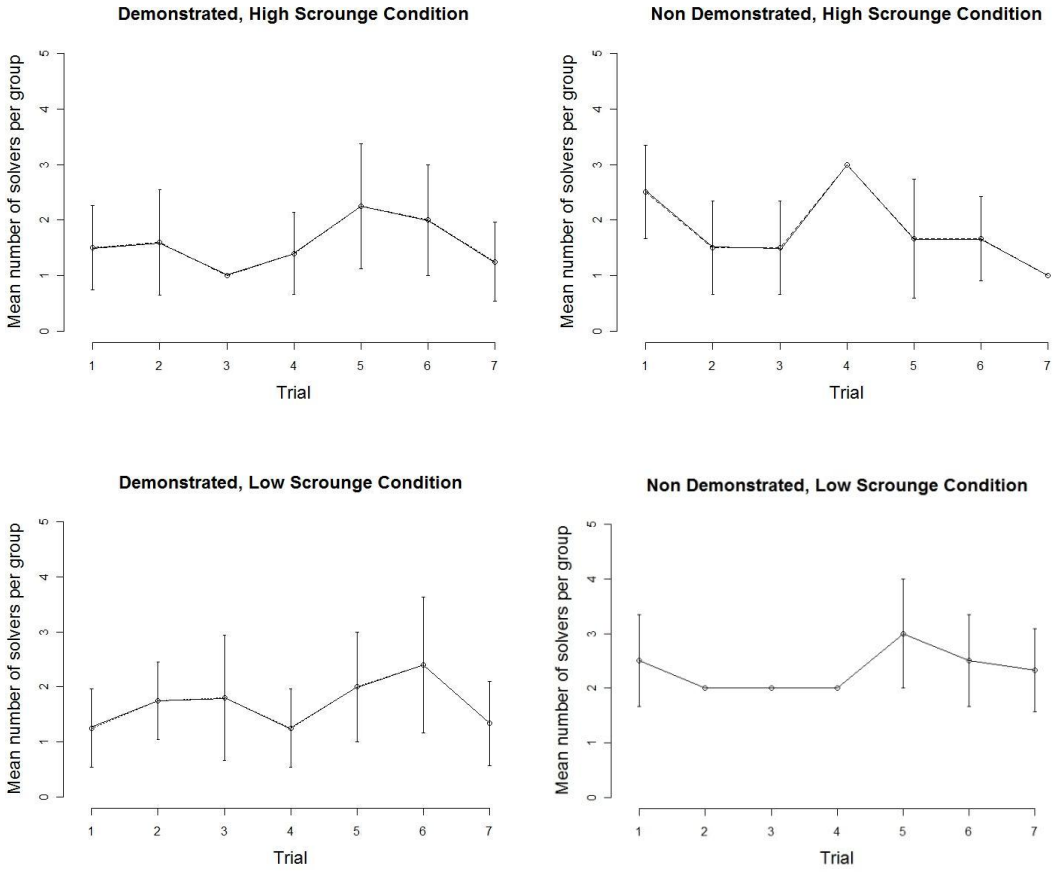


Figure 3.11: Number of solvers per group over trials 1-7 according to scrounge condition and demonstrator condition (mean ± SE).

In the *LMM* run to assess how evenly distributed (or more precisely, how unevenly distributed) task solving performances were amongst skilled group members under different conditions, the interaction between scrounge and demonstrator condition approached significance (t = -1.90, df = 62, p = 0.06). Groups' deviation scores differed relatively little across scrounging conditions in the presence of a demonstrator, being estimated at only 1.09x greater in high-scrounge conditions than

in low-scrounge conditions (95% CI = [0.82, 1.46]). In non-demonstrated conditions, though, deviation scores were markedly greater under high-scrounge conditions than low-scrounge conditions, being estimated at 1.71x greater in high-scrounge than low-scrounge conditions (95% CI = [1.19, 2.47]). The ratio of the effect between the two conditions was estimated at 1.56x higher in non-demonstrated conditions than in demonstrated conditions (95% CI = [0.98, 2.48]) (Fig. 3.12).

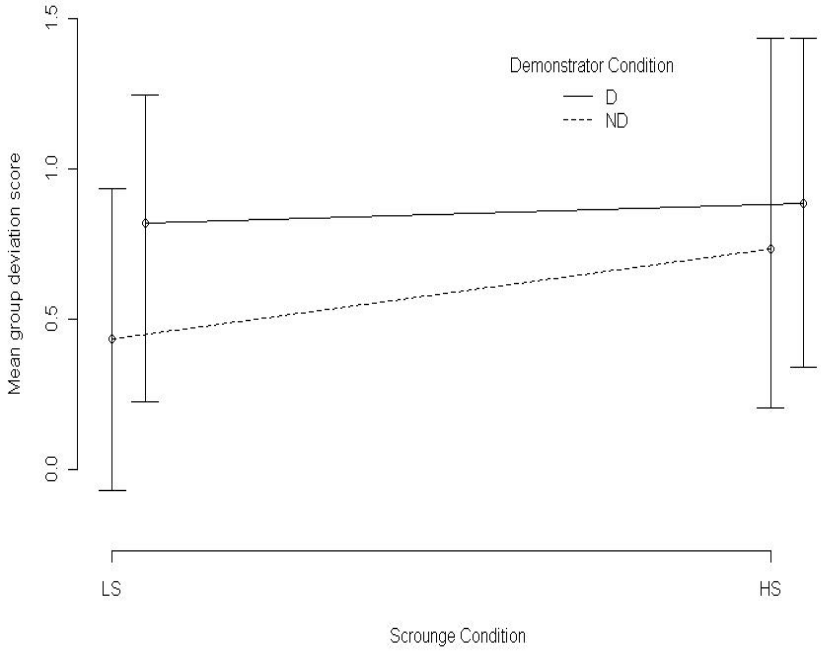


Figure 3.12: Extent of deviation from an even distribution of task solving behaviour (trials 1-7) among competent birds according to scrounge condition (LS, low-scrounge, HS, high-scrounge) and demonstrator condition (D, demonstrated, ND, non-demonstrated) (mean ± SE).

Production Behaviour (Trials 1-10)

In a *GLMM* including solving data across trials 1-10, the interaction between scrounge and demonstrator condition approached significance (Wald test: $z = 1.54$, $p = 0.12$).

The proportion of group members that performed at least one task solve differed relatively little across scrounging conditions in the absence of a demonstrator, with the odds of solving estimated to be 0.82x (95% CI = [0.29, 2.29]) greater in high-scrounge conditions than in low-scrounge conditions. In demonstrated conditions, though, a higher proportion of birds became task solvers under high-scrounge conditions than under low-scrounge conditions, with the odds of solving estimated to be 2.60x (95% CI = [0.91, 7.39]) greater in high-scrounge conditions than in low-scrounge conditions. The ratio of the effect between the two conditions was estimated at 3.17x higher in the demonstrated condition than in the non-demonstrated condition (95% CI odds ratio = [0.72, 13.88]) (Fig 3.13).

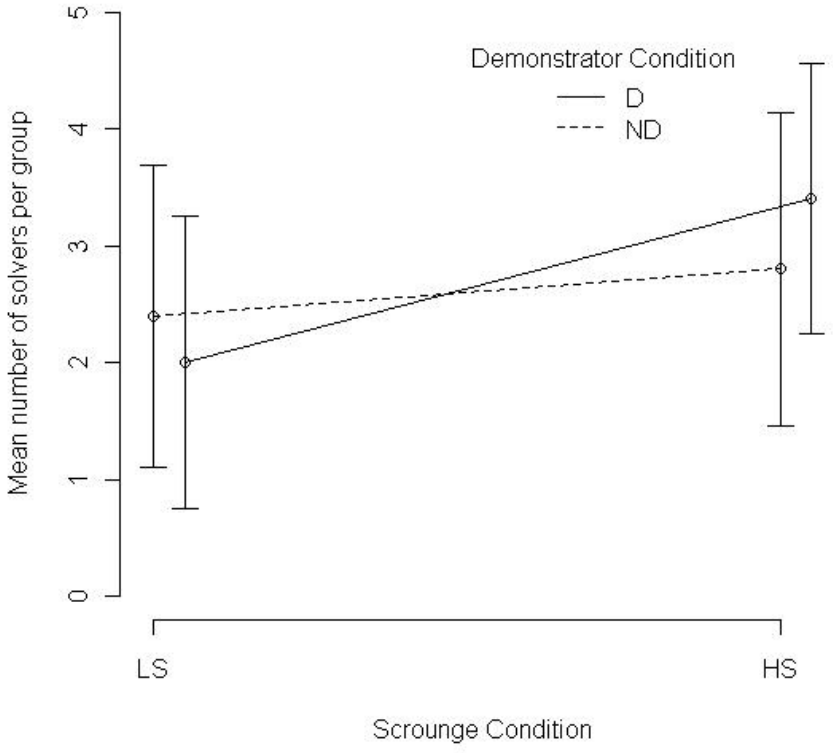


Figure 3.13: Number of solvers per group (trials 1-10) according to scrounge condition (LS, low-scrounge, HS, high-scrounge) and demonstrator condition (D, demonstrated, ND, non-demonstrated (mean ± SE).

In trials 8-10, at least one new task solver appeared in four of my five 'Demonstrator, High Scrounge' tests following demonstrator removal (six new solvers in total), whereas under 'Demonstrator, Low Scrounge' conditions, only one new task solver appeared across all five groups. In the two non-demonstrated conditions, only one group (in the high-scrounge condition) gained any new solvers (two in total) over the course of trials 8-10. Overall, more new solvers appeared under high-scrounge conditions, and under what had previously been demonstrated conditions, than under low-scrounge or non-demonstrated conditions (Fig. 3.14).

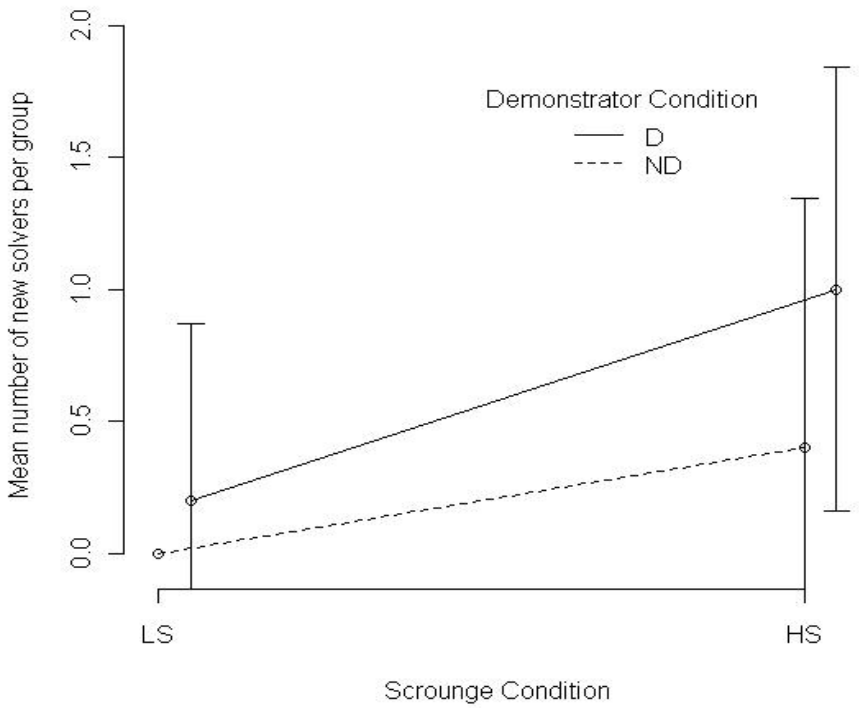


Figure 3.14: Mean number of new solvers per group (trials 8-10) according to scrounge condition (LS, low-scrounge, HS, high-scrounge) and demonstrator condition (D, demonstrated, ND, non-demonstrated) (mean ± SE).

A randomisation test, run to assess whether birds' task-solving activity increased, decreased or remained approximately constant in the latter stages of the experiment

(trials 8-10) compared to the early stages (trials 1-7), provided little evidence of an interaction between scrounge and demonstrator condition ($F = 0.16$, $p = 0.90$, 95% CI on p-value [0.89, 0.90]). Budgerigars in demonstrated conditions – most noticeably those in demonstrated, high-scrounge conditions – on average showed small increases in their task solving activity during trials 8-10 relative to trials 1-7 (i.e., following the removal of the demonstrator from their group), while birds under non-demonstrated conditions on average made very slight decreases in their solving activity during this time. This effect, however, was not significant ($F = 0.42$; $p = 0.38$, 95% CI on p-value = [0.38, 0.39]). There was also little evidence for an effect of scrounge condition on changes in birds' solving activity ($F = 0.58$; $p = 0.28$, 95% CI on p-value = 0.28, 0.29) (Fig. 3.15).

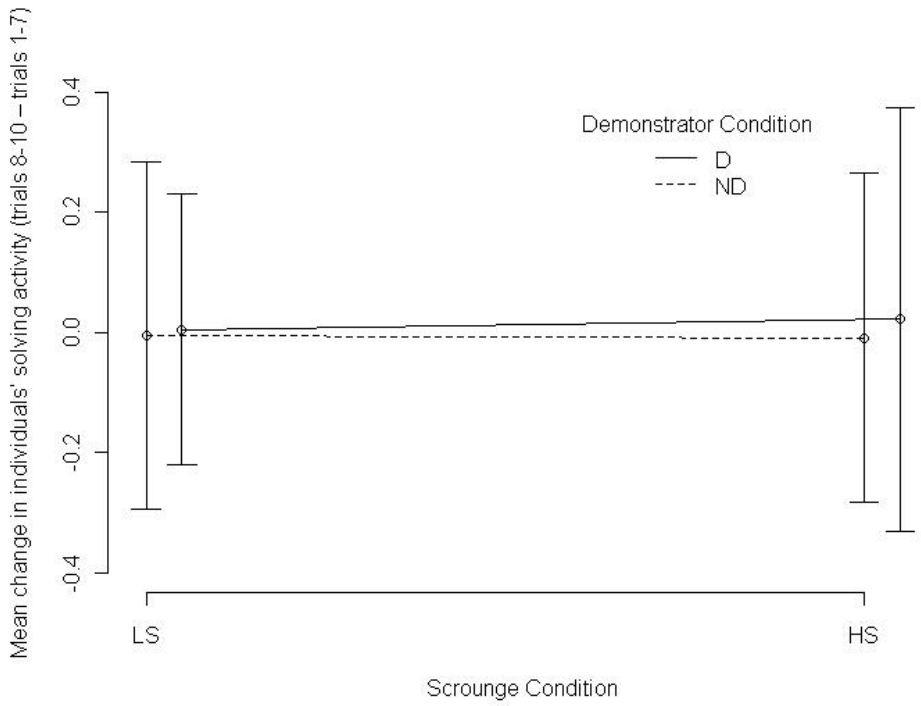


Figure 3.15: Change in individuals' task solving activity between early (1-7) and late (8-10) trials, according to scrounge condition (LS, low-scrounge, HS, high-scrounge) and demonstrator condition (D, demonstrated, ND, non-demonstrated) (mean ± SE).

Discussion

In this study, I presented five groups of seven to eight naïve budgerigars with four different foraging tasks, each under a different combination of scrounge and demonstrator conditions.

Predictions 1 and 2

Contrary to expectations, over the course of trials 1-7, I found no evidence of a difference in the proportion of birds that solved tasks (acted as producers or opportunists) under high-scrounge conditions compared to low-scrounge conditions (Fig. 3.6). This fails to support my first prediction, which was that a greater proportion of group members would act as producers / opportunistic producer-scroungers under low-scrounge conditions than high-scrounge conditions. It is possible that, whilst a greater proportion of birds may indeed have stood to benefit from adopting producer roles under low-scrounge conditions than high-scrounge conditions, opposing factors – such as solutions to tasks being possibly more difficult to initially acquire under low-scrounge than high-scrounge conditions – may have served to restrict the number of birds that were able to adopt production behaviour under low-scrounge conditions.

Having once solved a task, however, birds were significantly more likely thereafter to solve tasks repeatedly under low-scrounge and non-demonstrated conditions (especially under combined low-scrounge, non-demonstrated conditions) than under high-scrounge or demonstrated conditions (Fig. 3.11, 3.12). This offers support for

my second prediction, which was that birds would operate as producers / opportunist producer-scroungers more consistently (and not revert back to pure scrounging) when the scrounger's share was low.

Under all conditions, birds that acted as producers or as opportunists generally fed for longer than birds that operated only as scroungers. In absolute terms, producers and opportunists in high-scrounge trials fed for longer than producers and opportunists in low-scrounge trials. This went against my assumption that task solvers would have time to monopolise seeds for a roughly constant period of time before being displaced by other members of their group. The primary reason for this appeared to be that scroungers were typically somewhat slower to displace solvers from tasks under high-scrounge conditions, because the larger amount of food present in each task during high-scrounge compared to low-scrounge trials meant that scroungers also earned high absolute levels of reward, and took longer to deplete resources at existing solved tasks, which presumably reduced their incentive to dislodge producers from their most recently solved tasks quite so quickly as in low-scrounge trials. Despite differences in birds' absolute feeding durations, the feeding duration of producers and opportunists *relative* to scroungers was, as anticipated, still higher under low-scrounge than high-scrounge conditions (Fig. 3.4).

Together, these results imply that budgerigars were sensitive, at least to some extent, to the rewards reaped by producing versus scrounging under different conditions, and adjusted their behaviour accordingly. When scrounging yielded little reward (both relatively and absolutely low feeding durations), as in the non-demonstrated, low-scrounge condition, birds that acquired task solving skills appeared to be motivated to

repeatedly deploy these skills (even whilst, in the case of opportunists, apparently still remaining vigilant for possible scrounging opportunities), presumably to increase their food intake. When scrounging yielded high absolute levels of reward, as in both high-scrounge conditions, the majority of task competent birds in a group typically reverted to operating exclusively as scroungers after solving only one or two tasks by themselves. It is possible that birds' incentive to work as producers under rich scrounging conditions was low and that they tended to adopt a 'satisficing' strategy, remaining as scroungers (even though this was a sub-optimal strategy) so long as this yielded sufficient reward in order for some threshold criterion to be met.

These findings lend some support to Vickery *et al.*'s (1991) deterministic rate-maximising model of the producer-scrounger game, in which the equilibrium proportion of individuals in a group playing producer is higher when the producer's payoff is large, and the scroungers' payoff is small. The fact that birds that had learnt how to solve tasks sometimes acted as opportunist producer-scroungers during trials, rather than as pure producers, also lends support to Vickery *et al.*'s (1991) assertion that producing and scrounging need not necessarily be mutually incompatible foraging strategies. In this particular experiment, the close proximity of one task to another when arranged on a group's aviary floor may have made it possible for birds to search for already-solved tasks to scrounge from at the same time as searching for new tasks to potentially solve themselves, rather than have to specialise in once search mode over the other. The fact that the feeding durations of opportunists were typically only marginally shorter than those of pure producers (but significantly longer than those of pure scroungers) lends further support to this possibility. Interestingly, those birds that acted as pure producers were often demonstrators – birds that were highly

skilled at task solving from the outset of trials, and that may therefore have benefitted most from focussing their attentions mainly on looking for unsolved tasks to interact with and access food from, rather than from adopting an opportunist strategy and attempting simultaneously to look for tasks that had been solved by other members of their group, and scrounging from these. Notably, the condition with the greatest preponderance of opportunists relative to pure producers was the non-demonstrated, low-scrounge condition. Here, all birds were initially naïve, slow and unskilled at task solving. Therefore, whilst their incentive to develop their task solving skills in this condition was apparently high (see previous paragraph), so too may have been their incentive to remain vigilant for potential scrounging opportunities as a means of maximising their seed intake.

My findings in the demonstrated, low-scrounge condition require some further explanation. Here, birds' distribution of task solving behaviour was closer to that seen under high-scrounge conditions than under non-demonstrated, low-scrounge conditions (Fig. 3.12). Scrounging *was* somewhat more profitable than in non-demonstrated, low-scrounge conditions, due probably to the fact that demonstrators, highly proficient at solving tasks from the outset, often solved multiple tasks in rapid succession, sometimes moving on to a new task before fully exploiting (or being challenged by other group members for access to) the food available at the previous one. One possible reason for this seemed to be that demonstrators often appeared to find interacting with tasks intrinsically rewarding, and would occasionally feed at a task for only a short period of time before moving onto solving another one (even if no other birds had challenged them for access to their current one). In addition, demonstrators sometimes quickly abandoned one task and moved on to another –

rather than attempting to defend the one they were feeding at – once other group members arrived. Since they were already highly skilled task solvers, able to solve tasks quickly and efficiently, it is possible that demonstrators found it less costly to move on to as yet unsolved tasks when approached by other birds, than to engage in conflict with their fellow group mates over the contents of the task they were currently exploiting. In absolute terms, though, the rewards conferred by scrounging were still much closer to those conferred under non-demonstrated, low-scrounge conditions, and considerably lower than under either of the two high-scrounge conditions – suggesting that group members would have benefitted by engaging in production behaviour more frequently than most of them in fact did. A probable explanation for this result lies again in the speed with which demonstrators solved tasks. Such was this, that remaining group members may have had relatively little time to themselves interact with, and potentially produce food from, still unsolved tasks – even if they would have profited from doing so. This problem did not arise under non-demonstrated, low-scrounge conditions, since all group members were initially naïve, and required repeated trials before they were sufficiently skilled at producing as to be able to solve numerous tasks in rapid succession.

Interestingly, despite budgerigars exhibiting some flexibility in their tendency to solve tasks, seemingly dependent on the profitability of scrounging relative to producing / opportunist producer-scrounging, under no conditions did birds adjust their behaviour to the extent that the feeding durations of birds using each strategy ultimately converged, as has been found to occur in captive flocks of spice finches, *Lonchura punctulata* (Mottley and Giraldeau, 2000). Instead, producing / opportunistic producer-scrounging remained considerably more profitable than scrounging over

repeated trials across conditions (even for those demonstrators that occasionally left tasks before being challenged to access for them by other birds), suggesting that more individuals should have switched from scrounging to producing / opportunistic producer-scrounging, in order to maximise their food intake, than actually did.

I propose a number of possible reasons for this apparent shortage of task solvers. Firstly, as previously mentioned, birds may 'satisfice' and lack the motivation to work as task solvers so long as scrounging (despite being a sub-optimal foraging strategy) confers an adequate level of reward. It is also possible that there are costs, as well as benefits, associated with the acquisition and performance of new foraging skills, such as an investment of time and energy in the actions necessary to obtain food from the new source. Furthermore, though it may potentially confer large rewards, operating as a producer (searching for new foraging patches to exploit) – especially in the wild, where patches may be widely dispersed – may provide a less guaranteed supply of food than operating as a scrounger (scanning to see which group members have located food and then approaching them directly) (Giraldeau and Dubois, 2008). If the budgerigars in my study were sensitive not only to the mean, but also to the variance, of each strategy's payoff (Caraco, 1981; Stephens, 1981), then those in a good nutritional state (as most of my captive, well-fed birds should have been), for whom scrounging was likely to return a reliable and satisfactory payoff, may by-and-large have lacked the motivation or energetic need to adopt higher risk production behaviour (Caraco and Giraldeau, 1991).

It is also possible that the foraging tasks I presented to the budgerigars were sufficiently challenging as to mean any group's convergence towards an optimal ratio

of producers / opportunistic producer-scroungers to scroungers was very slow, and unable to be fully captured in the timeframe of my trials. Lastly, it may be the case that, when the rewards from scrounging and producing were both sufficiently high, birds were unable to discriminate reliably between strategies in terms of their relative payoff.

Predictions 3 and 4

Counter to my third prediction, budgerigars were generally no quicker to make their first task solve when their group contained a demonstrator than when it did not (Fig. 3.9). Demonstrators typically engaged with tasks shortly after they were presented, potentially generating opportunities for various forms of social learning to take place (for instance by drawing naïve group members' attention to tasks, the food within them, and/or the actions necessary to solve tasks) (Heyes, 1994; Hoppitt and Laland, 2008), as well as possibly helping to reduce any neophobia birds had towards the tasks (though given a period of pre-training prior to the commencement of full trials, groups' first exposure to complete versions of each task did not occur until their first proper trial). Whilst these actions might have been expected to result in naïve birds being faster to make their first task solve in the presence of a demonstrator, it is important to note that, since demonstrators were highly proficient at task solving, they often solved several tasks in quick succession at the beginning of every trial. Not only did this reduce the number of unsolved tasks available for the rest of the group to interact with, and potentially produce food from, but in cases where tasks were loaded with large amounts of food (high-scrounge conditions), it also created profitable scrounging opportunities. Thus, it seems likely that any positive effects that

demonstrations had on naïve birds' social learning of new production skills, may well have been counteracted by the reduced opportunities to interact with as-yet unsolved tasks, along with increased opportunities for scrounging, simultaneously conferred by the presence of a demonstrator in their group. In addition, the fact that demonstrators sometimes solved tasks without stopping to feed from them for long may have reduced naïve birds' capacity to associate task solving activity with the subsequent acquisition of a food reward. Thus, whilst such demonstrations might have facilitated some forms of social learning (e.g., stimulus / local enhancement), they may not have permitted others (e.g., observational conditioning / response-stimulus learning). This could be another reason why naïve birds under demonstrated conditions were typically no quicker to make their first task solve than those under non-demonstrated conditions. On the basis of the current experimental design, it is also impossible to rule out the fact that, since groups that contained demonstrators were larger than groups that did not, naïve birds under demonstrated conditions may have experienced greater competition for access to tasks, potentially reducing their ability to access and interact with them and thus hindering their ability to become task solvers themselves.

Whereas I had expected any positive impact a demonstrator had on its naïve group mates' acquisition of task solving behaviour to be more marked under low-scrounge than high-scrounge conditions (assuming birds would have a greater incentive to adopt production behaviour when the amount of food they gained through scrounging from a demonstrator's pre-solved tasks was small – my fourth prediction), I found no evidence of any difference between birds' first solve times under high or low scrounging conditions, in the presence or absence of a demonstrator (Fig. 3.11). This may indicate that budgerigars found it relatively more difficult to acquire new task

solving skills when scrounging opportunities were restricted (perhaps because it took them longer to develop sufficient associations between task objects and access to food, as to become sufficiently motivated to interact with, and attempt to solve, tasks by themselves), and that this effectively counteracted any increased 'production drive' birds experienced under low-scrounge conditions. Alternatively, it is possible that even the relatively low levels of reward birds obtained as scroungers under low-scrounge conditions may generally have been sufficient to meet their foraging requirements, and therefore have limited their motivation to adopt production behaviour.

Predictions 5 and 6

In accordance with my fifth prediction, I found some evidence that birds increased their task solving activity slightly once the demonstrator (generally the most; on two occasions the second most prolific producer in the group) was removed from their group, although this effect did not reach significance (Fig. 3.14, 3.15). The trend was predominantly attributable to a number of birds that had previously operated only as scroungers, adopting production behaviour for the first time after their demonstrator was taken away. By contrast, very few new solvers appeared in groups that did not lose a producer, suggesting that their emergence was not solely the result of continued exposure to the tasks over the course of an additional three trials. Rather, the appearance of new solvers in groups from which an existing solver had been removed implies that birds possessed some level of sensitivity to the rewards of producing in comparison to scrounging, and could to a certain extent adjust their use of each strategy depending on its current profitability.

Unfortunately, the experimental design used here leaves open the possibility that birds in demonstrated groups may have altered their task solving behaviour not (only) for the above reason, but in response to the alteration in their group dynamics, or a reduction in competition for access to tasks, caused by the removal of the demonstrator from their group. An improved design could include the placement of a 'sham' demonstrator (naïve bird) in non-demonstrated groups, to be removed at the same point as real demonstrators (i.e., at the end of trial 7), in order to control for the latter two possibilities. Such a design would itself, however, rely on sham demonstrators not becoming proficient task solvers themselves – if they did, their removal from groups might be akin to removing a real demonstrator. An alternative might be to separate and attempt to train an existing member of a group to solve a particular task (though there would be no guarantee the bird selected would learn to become a competent task solver, as individuals appeared to vary considerably in their task solving ability – see Chapter Four), and then return it to its group to act as a demonstrator. This bird (or perhaps whichever member of the group proved to be its most prolific producer, if not the demonstrator) could then be removed from the group at the end of trial 7, as could one non solving bird from an equivalent group under non-demonstrated conditions.

Despite the limitations of the experimental design used here, the emergence of new, first-time solvers following demonstrator removal was somewhat more marked in groups under high-scrounge conditions than in groups under low-scrounge conditions, although again this effect did not reach significance. Since all other factors (disruption to group dynamics; alteration in levels of competition for access to tasks) ought to have been roughly equivalent across groups under demonstrated conditions – and all

that differed between them was the amount of food that was presented inside tasks (large amounts in high-scrounge conditions versus small amounts in low-scrounge conditions), this finding offers some support for the concept that scrounging may facilitate individuals' underlying learning of skills, even whilst possibly suppressing their expression of these skills until such a time as scrounging is no longer rewarding (my sixth prediction). Unlike Giraldeau and Lefebvre (1986), Beauchamp and Kacelnik (1991), and Giraldeau and Helder (1997), I found no evidence to suggest that scrounging inhibited learning.

A key difference between this study and earlier work, which found scrounging to have an inhibitory effect on learning (Giraldeau and Lefebrve, 1987; Nicol and Pope, 1994), is that in this case, high-scrounge and low-scrounge conditions were generated simply by varying the amount of food inside tasks, leaving all other aspects of the set-up completely identical (i.e., all trials consisted of free conditions in which birds could interact without restraint). More traditionally, such conditions have been reserved for the scrounging component of experiments, with non-scrounging conditions being enforced by physically preventing birds from directly interacting, usually by means of screens or partitions. Since my findings suggest that, all else being equal, scrounging does *not* appear to inhibit birds' learning (if anything, the opposite), it is possible that the seemingly contradictory results obtained in previous studies may be due largely not to scrounging *per se* inhibiting learning, but to 'open' – more naturalistic – conditions generating more confusion and/or aggression than those in which animals are prevented from directly interacting with one another.

Extensive scrounging from already-solved tasks may have aided budgerigars' acquisition of production skills in a number of ways. Since they spent more time in close proximity to tasks when there were large amounts of food available to scrounge, birds may have had more opportunity to form associations between tasks and food under high-scrounge conditions. This in turn may have increased their motivation to interact with tasks to access food from them by themselves when no longer able to rely on a demonstrator to do the work for them, much like the meerkats, *Suricata suricatta*, in Thornton and Malapert's (2009) study. Furthermore, in the free conditions under which this study was conducted, the confusion and scramble-competition experienced by naïve birds when attempting to scrounge food from previously solved tasks, may have limited their ability to detect which member of their group was responsible for having solved the task in question. Whilst potentially ruling out some forms of social learning, such as imitation, observational conditioning or observational response-stimulus learning, this may have helped to prevent birds from developing associations between specific producers and food, as opposed to between task objects and food, which might otherwise have compromised (overshadowed) their ability to acquire task solving behaviour themselves.

Conclusions

Superficially, new behaviours may seem to be taken up by animals in groups equally well (or equally poorly) regardless of the scrounging opportunities available. However, this study illustrates that learning a new skill is not necessarily synonymous with performing it, and should not be treated as such.

In this study, budgerigars appeared to be able to 'play' the producer-scrounger game opportunistically, operating predominantly as scroungers so long as this foraging strategy conferred sufficient reward, and adopting production behaviour only when it did not. While apparently suppressing birds' immediate, or at least repeated, expression of new foraging skills, scrounging ultimately appeared somewhat to enhance their ability to act as producers when the need arose.

When tracking the diffusion of innovations through populations, it is therefore important to consider the possibility that, should they fail to spread, this may not be due to a failure by animals to learn them, but to animals deferring their performance of new skills until such a time as they become sufficiently profitable to express.

Further Work

In addition to improvements already mentioned (e.g., the inclusion of sham demonstrators in groups), a number of further refinements / extensions could be made to the work presented here.

An implicit assumption of this work has been that birds' feeding durations at tasks corresponded directly to their actual food intake. It is possible, however, that tasks delivered diminishing returns as their seed supplies became depleted. As such, though difficult, it would be useful to try and measure the number of seeds birds actually ate during a foraging bout, rather than simply timing how long their beaks were in contact with the millet clusters inside tasks.

It could also be beneficial to devise a set of tasks that were able to vary the amount of food they dispensed to the bird that first solved them (the producer's share) whilst containing a constant overall amount of food. Such an approach might offer greater control over the relative profitability of producing and scrounging, and allow greater insight into whether birds' primarily paid attention to the relative or the absolute payoff of producing / scrounging when selecting a foraging strategy, than was possible with the cruder method used here, in which different absolute quantities of food were provided to generate high-scrounge and low-scrounge conditions.

Furthermore, this work has only examined birds' responses to the removal of one bird (the demonstrator) from their group. In its current form, the experiment required only one remaining member of groups that had lost their demonstrator to increase its task solving activity to compensate for the demonstrator's removal, before all other members could revert to scrounging or opportunistic producer-scrounging much as before (indeed, this was main reason why groups received only three further trials – rather than, for instance, a further seven – following their demonstrator's removal). Sequential removal of birds from groups as and when they became proficient producers – or removal of several producers at once – might, in a future experiment, provide increased insight into the behavioural flexibility of scroungers in response to the loss of producers from their groups (for further discussion of this possible avenue of research, see Chapter Seven).

I also suggest that further research is now needed into group producer-scrounger dynamics under a greater range of conditions (for instance, where the 'cost', or difficulty, of producing is either raised or lowered, and among different sized groups

of animals). Investigation of individual level traits, such as age, sex, body condition, and position within a group's hierarchy, as potential predictors of an animal's tendency to adopt the role of task solver (producer / opportunist producer-scrounger) or of non task solver (scrounger), is also likely be illuminating, and is explored in the following chapter.

CHAPTER FOUR

INDIVIDUAL-LEVEL PREDICTORS OF PRODUCING AND SCROUNGING BEHAVIOUR

Abstract

To date, few studies have looked explicitly at what, if any, individual level characteristics influence an animal's likelihood of behaving as a producer (or as an opportunist producer-scrounger), rather than as a pure scrounger when foraging in a group. It has been postulated that individuals may form 'skill pools', in which different animals act as producers under some foraging circumstances, and as scroungers under others. Alternatively, it is possible that certain individuals may possess attributes that dispose them to acting as producers in numerous different situations, whereas others operate as habitual scroungers.

Here, I examine the producing behaviour of small-group-housed budgerigars, *Melopsittacus undulatus*, presented with four different novel foraging tasks. I also measure a number of each bird's individual level characteristics, including its age, sex, body condition, response to a novel object, asocial learning ability, and competitive rank within its group, as well as its mean interaction times with, and scrounge durations from, each of the four group foraging tasks presented to it.

I find little evidence to suggest that budgerigars developed skill pools. Rather, certain birds exhibited production behaviour across a variety of contexts, while others consistently acted as scroungers. Competitive rank, sex, interaction time with, and scrounge duration from foraging tasks, were found to be useful indicators of an individual bird's propensity to adopt production behaviour.

Introduction

Theoretical models of the producer-scrounger game tend to assume, perhaps rather unrealistically, that individual foragers are equally able to use each strategy and that the payoffs they reap from adopting one or the other are independent of characteristics such as their place in a group dominance hierarchy (Beauchamp, 2001). Meanwhile, only a handful of empirical studies have looked for correlations between an animal's strategy use and a range of individual traits (most often, its place in the group dominance hierarchy) (e.g. Baker et al, 1981; Barnard and Sibly, 1981; Rohwer and Ewald, 1981; Czikeli, 1983; Beauchamp, 2006).

In Chapter Three, I presented five groups of six to eight captive budgerigars, *Melopsittacus undulatus*, with four different types of foraging tasks loaded with millet seeds. Birds could act as 'producers', accessing food from these tasks by interacting directly with them (for instance, by lifting a lid, or pulling out a drawer to reveal food). Alternatively, they could act as 'scroungers', exploiting the efforts of the producers in their group either by actively displacing them from tasks they had recently solved and stealing the rewards within, or by consuming any seeds remaining inside tasks that had already been solved, but to which producers were no longer attending. Some birds also acted as 'opportunists', using a combination of producing and scrounging behaviour within one foraging session. For the purposes of this chapter, any bird that managed to access food from a particular type of task at least once by itself (whether or not it subsequently operated as a pure producer or an opportunist) will be treated as a producer. Birds that never once accessed food from a

particular type of task by themselves, but fed solely from tasks that had been solved by other members of their group, will be treated as scroungers.

Here, I investigate (a) whether certain birds adopted production behaviour across a variety of foraging contexts, whilst others operated solely as scroungers across presentations of different foraging tasks; and (b) if so, whether their tendency to adopt producing or scrounging roles correlated with individual level characteristics such as age, sex, and competitive rank.

According to the 'skill pool' hypothesis proposed by Giraldeau (1984), 'individuals within foraging groups may have different repertoires of foraging behaviours, each specialising on a sub-set of a population's diet range.' Any given individual in a group is assumed to possess a subset of the foraging skills possessed by the group as a whole, such that individuals that act as producers when foraging on subset '*A*' will act as scroungers when foraging on subset '*B*' and vice versa, and such that 'the searching efficiency of an individual foraging on subset '*A*' will profit individuals foraging on subset '*B*' and vice versa', (Giraldeau and Dubois, 2008). In order for a foraging skill pool to arise, it is possible that multiple individuals in a group would need to possess similar levels of ability and inclination to solve novel foraging problems. In addition, individuals' arrival times at new food sources would presumably need to be such that in some instances, particular individuals happened to arrive early at (and begin investigating, interacting with, and producing food from) new food sources encountered by the group, whereas in others, the same individuals happened to arrive later, joining (and scrounging from) other members of their group that had already discovered, and successfully accessed, the new food source. An alternative means by

which a skill pool might arise would be if certain members of a foraging group possessed greater levels of ability or inclination than others to solve particular types of novel foraging problem (e.g., problems involving pulling), whilst other members of the group preferred, or were better at solving, different foraging problems (e.g., problems involving pushing). Contrastingly, should certain individuals generally be better at solving novel foraging problems than others, and/or tend to be quicker to investigate new foraging areas than others, the formation of a skill pool would be unlikely.

A limited amount of empirical support exists for the skill pool hypothesis. In a study using a captive flock of feral pigeons, *Columba livia*, Giraldeau and Lefebvre (1986) found evidence of birds adopting distinct producer and scrounger foraging roles within a specific foraging patch. These roles, however, were not fixed across different foraging contexts. The identity of the individual birds operating as producers and scroungers differed according to which of three different types of food patch was being presented. Birds that had previously acted as scroungers were also found to be capable of switching to producing if their flock composition was altered. Moreover, adoption of one role or the other bore no relation to a bird's individual learning ability, or its position in the flock's dominance hierarchy (although the latter may have been because the foraging patches used in this experiment were not of the type that could be monopolised by a single individual – if they had been, it is possible that social rank may indeed have been important).

While skill pools may sometimes develop, it is also possible that certain individuals in a foraging group may be predisposed to operate as producers, whilst others may be

more likely to operate as scroungers (Giraldeau and Dubois, 2008). It follows that their favoured strategy may depend on such characteristics as age, sex, rank and possibly 'personality'. For instance, in Harris' sparrows, *Zonotrichia querula*, dark-eyed juncos, *Junco hyemalis*, and domestic pigs, *Sus scrofa domesticus*, only dominant individuals tend to scrounge (Baker *et al*., 1981; Rohwer and Ewald, 1981; Czikeli, 1983; Held *et al*., 2010), while in zebra finches, *Taeniopygia guttata*, Beauchamp (2006) found that individuals with low foraging efficiency were more likely to scrounge from other birds when given the opportunity.

Although relatively few studies have examined phenotypic differences in individuals' foraging behaviour specifically within the context of producing and scrounging, studies of animal innovation (and the characteristics that may predispose an individual to become an innovator) are more numerous. Reader and Laland (2003) define innovation in two ways: as a 'new or modified learned behaviour not previously found in the population' (innovation *sensu* product), and/or as a 'process that results in a new or modified learned behaviour and that introduces novel behavioural variants into a population's repertoire' (innovation *sensu* process). The two definitions are subtly distinct, since the *process* of innovation is not the only means by which a novel behaviour may be introduced into a population – immigration into a population of an animal exhibiting a new behaviour, or social learning of a new behaviour from some external source, can both achieve the same result. In addition to innovation, other authors (e.g., Slater and Lachlan, 2003) have defined 'invention'. This is often treated as a process distinct from innovation, involving 'a behaviour pattern that is totally novel, not obviously derived from one that an animal has been exposed to', whereas innovations are 'new behaviour patterns derived by modifications to previous ones'

(Slater and Lachlan, 2003). Inventions might also be considered as the creation of new ends, whereas innovations are simply novel ways of obtaining the same end (Ramsey *et al.*, 2007). Ramsey *et al.* (2007) further suggest, however, that inventions might best be categorised, not as qualitatively distinct from innovations, buts as a sub-set of innovations that are rarer, more novel, and involve more cognition than other, 'weaker' innovations – in essence, the 'pinnacle' of innovation.

Innovation (*sensu* product and process), defined here in the broadest sense to include invention, can enable an animal to solve novel problems, or to solve existing problems in a new way (Köhler, 1925; Hinde and Fisher, 1951; Kummer and Goodall, 1985; Laland and Reader, 1999; Reader and Laland, 2003). It may enable animals to exploit new resources, utilise familiar resources in a more efficient manner, withstand environmental change, and invade or construct new niches (Reader and Laland, 2003; Sol *et al.*, 2005; Ramsey *et al.*, 2007). Over time, innovations may sometimes spread through animal groups, resulting in the formation of local traditions (Reader and Laland, 2003).

In my study, 'demonstrator' birds that were already skilled at solving particular foraging tasks, and that were present in budgerigar groups when certain foraging tasks were presented to them (see table 3.1, Chapter Three for full details), were able to introduce innovations (*sensu* product) into their new groups. In the absence of a demonstrator, the first bird to successfully solve (produce food from) a new type of task, was an innovator (*sensu* process). Any other group members that subsequently acquired production skills were not, strictly speaking, innovators. They were not the first in their group to perform task solving behaviour, and could, potentially, have

acquired their skills by means of social learning. That said, it is possible that both innovators and producers shared some innovative attributes that differentiated them from birds that never solved, or were very slow to solve, tasks. All producers, whether or not they were the first in their group to yield food from a task, presumably had to possess a certain amount of motivation to approach and interact with it. Furthermore, at least some of them may have acquired their production skills via independent trial-and-error, rather than by social learning from the innovator, or any other producers, in their group.

If innovation is driven by necessity, as various data suggest (Reader and Laland, 2003), then the lowest-ranking, least competitive members of a group might be expected to be its most innovative. Since innovation is likely to involve risks (potentially wasted time and energy and/or exposure to danger), it may be that the animals most likely to take them, and invest their efforts in novel problem solving, are those at a competitive disadvantage and in greater need of resources than higher ranked individuals (Reader and Laland, 2003). Empirical support for this idea has been found in fish (Laland and Reader, 1999a,b); birds (Biondi *et al*., 2010; Morand-Feron *et al*., 2011; Cole and Quinn, 2012); meerkats, *Suricata suricatta* (Thornton and Samson, 2012); and primates (Reader and Laland, 2001, Kendal *et al*., 2005). It is worth noting, though, that other studies (e.g., Boogert *et al*., 2006, in a study of foraging innovation in small groups of captive starlings, *Sturnus vulgaris*) have found a positive correlation between rank and innovation. Thornton and Samson (2012) note that, in some species, it may be the case that individuals are able to achieve high status directly on account of their innovativeness.

With specific regard to the producer-scrounger game, dominants are usually expected to reap greater rewards from scrounging than subordinates, especially when food is clustered in patches from which dominants can displace subordinates, and then proceed to monopolise (Barta and Giraldeau, 1998). In order to obtain sufficient food, it may be necessary for subordinate animals not only to act consistently as producers, but also to innovate new foraging methods. Consistent with this prediction, a number of empirical studies have found that food discoverers tend to be subordinate individuals, frequently displaced from food patches by more dominant ones that then steal the resources they have made available (e.g. Bugnyar and Kotrschal, 2002a; Liker and Barta, 2002) – although others (e.g. Giraldeau and Lefebvre, 1986; Beauchamp, 2006) report no such effect.

In addition to dominance, characteristics that may plausibly affect an animal's tendency to innovate include its age, sex, body condition, asocial learning ability, neophobia level (the extent of its aversion to novel stimuli), exploratiVeness and/or tendency to scrounge. Thornton and Samson (2012), for example, found subordinate adult meerkats to be the best at solving novel foraging puzzles. Dominant adults rarely interacted with the puzzles at all (instead they exploited the discoveries of others by scrounging), and juveniles, though keen to interact with them, tended to lack the dexterity required to produce food from them. In addition, males (the dispersing sex) were more likely to innovate than females. Meanwhile in guppies, *Poecilia reticulata*, competitive ability is related to sex (Laland and Reader, 1999b). Males, which are smaller than females, are less successful at obtaining food during scramble competition. While Laland and Reader (1999b) found no evidence that foraging innovations were correlated with rank among female guppies, they did find them to be

inversely correlated with rank among males. In Boogert *et al.*'s (2006) study on captive starlings, innovators were usually characterised by their high rank, good asocial learning ability, and low levels of neophobia; while Benson-Amram and Holekamp (2012) found that juvenile hyaenas, *Crocuta crocuta*, were generally less neophobic, more explorative, and more persistent at engaging with a novel food-containing object than were adults.

The 'spare time' hypothesis (Kummer and Goodall, 1985) predicts that animals in good condition – such as captive animals or well-provisioned young – freed of the demands of routine foraging and equipped with an excess of energy, may exhibit higher-than-average levels of innovation (though Benson-Amram *et al.*, 2013, found no support for this in their study on captive hyaenas). Alternatively, it is possible that innovation may be associated with hunger (e.g. Laland and Reader, 1999a) – though in general, studies have found little correlation between an animal's body condition and its likeliness to innovate (e.g. Boogert *et al.*, 2010; Overington *et al.*, 2011; Morand-Ferron *et al.*, 2011).

Furthermore, an animal's personality may play an important part in its tendency to innovate. Personalities, or 'behavioural types', are inter-individual differences in behaviour that are consistent over time and across situations (Dingemanse *et al.*, 2002; Sih *et al.*, 2004a,b; Réale *et al.*, 2007). A population or species can exhibit a behavioural syndrome with each individual showing a behavioural type (for instance, being comparatively bold or shy; aggressive or non-aggressive; explorative or non-explorative) (Sih *et al.*, 2004a). Behavioural syndromes can potentially cut across categories such as age, sex and dominance, although members of different categories

(e.g., males versus females) may differ in their average degree of, for instance, shyness and boldness (Wilson *et al.*, 1994). Some of the most detailed work carried out thus far on behavioural syndromes has been with great tits, *Parus major*. Initial work found that birds displayed consistent individual differences in exploratory behaviour (activity in an unfamiliar environment). Relative to 'slow' explorers, 'fast' explorers were also more aggressive (Verbeek *et al.*, 1994), less neophobic (Verbeek *et al.*, 1996) and more likely to form routines (Verbeek *et al.*, 1994; 1996). Moreover, artificial selection over four generations produced fast, bold, proactive birds versus slow, shy, reactive birds, demonstrating that personality types were heritable (Drent *et al.*, 2002).

It is possible that individuals with particular personality types may display a heightened tendency to innovate relative to other members of their species. In rainbow trout, *Oncorhynchus mykiss*, for example, bolder, fast exploring individuals have been found to acquire information about novel situations and learn novel tasks more rapidly than shyer, slower explorers (Sneddon, 2003).

In this chapter, I tested the following predictions:

1) That certain budgerigars would consistently innovate / act as producers across a range of different foraging situations (i.e., that no skill pools would form).
2) That innovators / producers would typically share one or a number of characteristics, including their age, sex, body condition, response to a novel object, asocial learning ability, competitive rank, persistence / exploratiVeness, and/or (lack of) tendency to scrounge.

Methods

Innovation Measures

The group foraging experiments conducted in Chapter Three consisted of multiple copies of four different types of task (the 'Tube', 'Flap', 'Lucky Dip', and 'Drawers' tasks), each of which was presented a total of 10 times to five groups of budgerigars containing six to eight naïve individuals plus, in half of all cases, one competent demonstrator.

Here, I use the data I obtained during trials 1-7 of each task presentation to each group to provide information regarding: (a) whether or not individual birds solved, and produced food from, a particular task during this time, and (b) if so, how quick they were to make their first solve. Since each group (and therefore each bird) was presented with four different types of foraging task, these data can be used to assess whether the same group members tended to be responsible for solving tasks across a range of foraging situations, or whether different birds adopted the role of producer when different tasks were presented to their group. Note that data from trials 8-10 of each task presentation were not used here, since demonstrators, when present, were removed from groups during this time, potentially disrupting group dynamics and altering the behaviour of remaining group members (see Chapter Three for full details).

Each given task type was not presented to every group in an identical fashion. Rather, each task was presented to some groups in the presence of a pre-trained demonstrator

bird, and to others without; and in addition, some groups received a large portion of millet seeds stocked in the task, whilst others received only a small portion of seeds (see Table 1, Chapter Three for full details). However, in terms of assessing the consistency, or otherwise, of individual birds' tendencies to act as task solvers under different foraging circumstances, this should not be problematic because:

1) Over their course of task presentations, all groups were exposed to every one of the four possible combinations of demonstrator condition and seed-portion size (albeit in conjunction with different specific task types depending on the group in question). Thus, no particular effect of one specific combination of conditions should be significantly more marked in one group (and among certain individuals) than any other.
2) Furthermore, my results in Chapter Three indicated that during trials 1-7, no more, or fewer, birds solved tasks under one particular combination of demonstrator / seed-portion conditions than any other.

Time Spent Feeding on Millet Spray (Competitive Rank)

I attempted to calculate birds' competitive ranks within their groups using a similar method to Boogert *et al.* (2006; 2008), grading individuals on their ability to access and monopolise a highly valued resource (millet spray).

After a one hour period of food deprivation (water remained available throughout), I pushed a single millet spray through the mesh of a group's enclosure, next to a perch that only one or two individuals could access at a time, and set up a video camera for

10 minutes to record which birds fed from the millet spray. During video analysis, I recorded the total time each individual spent feeding from the millet spray during this time.

For each group, I collected 10 sets of feeding duration data three times over: both times the group contained a new member (a demonstrator), and again during one of its two non-demonstrated group foraging experiments. (Ideally, feeding duration data would have been collected for both non-demonstrated experiments; however, I wanted to prevent exposing the budgerigars to excessive quantities of millet spray over a short period of time – especially since the Tube, Flap, Lucky Dip and Drawers tasks all also involved the presentation of millet. Moreover, data collected during an earlier set of experiments (Hoppitt *et al.*, manuscript in preparation) suggested that group members' feeding duration ranks tended to remain relatively constant over repeated samplings, even following temporary disturbances – such as the insertion and removal of demonstrators – to their composition.) Data were only collected from groups containing a demonstrator once the demonstrator had undergone its three day acclimatisation period to the group. Since demonstrators were only present in groups for seven days following their acclimatisation, I collected one set of data in the early afternoon (at 1200 hours or 1230 hours, depending on which room the group was housed in – see Chapters Two and Three for further details) of a trial day, and a further one later in the afternoon (at 1400 hours or 1430 hours) on days one, three, and five of the group's trials. When there was no demonstrator present, I conducted this test once a day (at 1200 hours or 1230 hours) for the duration of the 10 day experiment.

The amount of time each bird spent feeding from the millet spray, summed up across all 10 trials, was converted into a rank. The individual that fed for the longest total time was ranked '1', and the bird(s) that fed for the shortest length of time, or not at all, was ranked '7', '8', or '9', depending on the size of the group. (Note that in cases where more than one group member failed to feed, birds were assigned tied bottom ranks, e.g. 6.5 or 7.5.) This figure was then transformed to allow for different group sizes, by calculating Rank = (Rank-1)/(N-1), where N was the number of birds in the group. This produced an index varying from 0 (highest ranking) to 1 (lowest ranking).

Asocial Problem Solving Ability

To obtain a measure of each budgerigar's ability to solve a novel foraging problem by itself when housed alone, I created a fifth foraging task, the Jar task (Fig. 4.1). This was presented to single birds after all groups had participated in all four of their group trials (the Tube, Flap, Lucky Dip, and Drawers tasks – see Chapter Three).

Figure 4.1: The Jar task, pre-training (left) and test (right) presentation.

As with the group tasks that had previously been presented to them, budgerigars were pre-trained to feed from a simplified form of the Jar task while still housed in their groups, and were exposed to four replicates of this simplified version of the task for a

minimum of three one hour sessions. When birds had been seen to feed from this at least once, they were transferred in pairs (pilot studies showed that they adjusted more rapidly to their new environment if introduced as a pair rather than singly) to a smaller test cage (30 cm W x 90 cm L x 40 cm H) containing perches, cuttlebone, and two bowls of food and water. This test cage was located in the same room as the birds' home group, orientated such that birds in the test cage could not see birds in group cages, and vice versa – but permitting the maintenance of auditory contact between all birds. Birds were transferred to the test cage at 1600 hours or 1630 hours (two hours before lights out, giving them time to adjust to, and feed in their new environment before the end of the day) the day before testing began. During this time, a pre-training version of the task was left in the cage, and experiments only began once food had clearly been eaten from this.

At 1200 hours / 1230 hours the next day, food bowls were removed and an opaque wooden board was inserted into the cage from front to back to divide it in half lengthways, leaving one bird in each compartment.[1] After one hour's food deprivation, each bird was provided with a test version of the jar task, and a video camera was set up to record its activity over the next four hours. Water and perching material remained available to both birds throughout the food deprivation and testing

1 Doing this incurred the potential problem of (visual) isolation stress in test subjects (birds remained in auditory contact with one another at all times). Pilot studies from a previous experiment (Hoppitt *et al.*, manuscript in preparation) had involved test birds being transferred to a test cage identical to that described above, in which a companion, not test subject, was already present. The test bird was then left to acclimatise to its new surroundings as already described. When testing began, the test bird and its companion were separated, one in each half of the test cage, using a piece of wire mesh (rather than the opaque wooden board used here). This ensured the two birds were physically separated, such that the companion bird could not interact with the task/object being presented to the test bird – but that birds remained in visual contact with one another. Unfortunately, so long as birds remained in visual contact with one another, the test bird typically paid very little attention to the task/object in its half of the cage, and instead attempted to re-establish physical contact with the companion bird on the other side of the wire mesh divider. In all, the presence of a companion served to reduce birds' inclination to interact with the task/object being presented to them, and if anything, appeared to increase rather than decrease their anxiety. Therefore, in this study, I temporarily housed test birds in visual isolation, but ensured that the length of time for which they experienced this was kept as short as possible.

period. At 1700 hours / 1730 hours, filming was stopped, the divider was removed, and food was returned, giving the pair one hour to feed *ad libitum* before lights went out.

The task itself was composed of a small (4 cm H x 3.5 cm diameter) glass jar, open at one end and closed at the other, tipped on its side and fastened to a 10 x 10 cm white cardboard base with two pieces of transparent tape. The inside of the jar contained millet seeds, which were accessible from one end of the jar.[2]

During pre-training, four jars were presented at one side of a group's home cage with their open ends facing in to the middle of the floor and pieces of millet spray protruding from these, such that when birds alighted on the floor to feed, millet was readily accessible in front of each jar. During test presentations, a small cluster of millet seeds was placed towards the solid end of the jar. On the floor of the test cage, the jar was rotated 180° so that its closed glass base now faced into the middle of the cage. To access the seeds within, birds now had to reach their heads into the open back of the jar. Since jars were transparent, birds tended to spend some time pecking at their solid base and sides in an attempt to reach the seeds within them before they (in some cases) then discovered the opening at the back.

[2] I had originally intended to present individuals with a much more comprehensive battery of asocial learning tests as per Boogert *et al*., 2010, 2011, who measured how many trials birds required to: be shaped to perform a novel motor task; learn a colour association; learn to reverse this; and exhibit sufficient inhibitory control as to succeed at a detour-reaching task (see also Hauser, 1999; Mischel *et al*., 1999; Vlamings *et al*., 2010). Unfortunately, however, early pilot work with the birds in my study established that, when housed on their own, they were (a) generally slow to engage with tasks in the first place, and (b) having once engaged with them, liable to soon lose interest in them if they did not succeed in obtaining food rewards from them almost straightaway. The timeframe that would have been required to shape the behaviour of 37 birds to solve a novel task – let alone subsequently measure their ability to learn colour associations and reversals – was therefore not practical. It would also have carried ethical concerns, since birds often exhibited some degree of separation anxiety when housed alone. Instead, I decided to present birds with a very simple task, to which they could be habituated whilst still in their groups, and which they could conceivably solve within a single test session when housed individually. Though undoubtedly at most a very crude measure of asocial problem-solving ability, this seemed preferable to no measure whatsoever.

Video footage was watched back using Windows Media Player, and I recorded (a) how many seconds each bird spent contacting the jar prior to accessing food from it for the first time, and (b) whether or not it solved – successfully accessed food from the jar – within the four hour testing period. (Note that birds were usually much slower to interact with tasks when housed alone than when housed in a group, which was why the Jar task was presented for a lengthier time than were the Tube, Flap, Lucky Dip or Drawers tasks during group task presentations.)

Task contact: an individual orientated towards and touching or manipulating any part of a task (excluding the cardboard base) with its beak or foot, but failing to solve (access food from) it. Instances of a bird perching on a task to take-off from the floor, landing on a task following flight, or brushing past a task with the body or tail when moving about on the aviary floor, were not counted as contacts.

Task solve: an individual reaching into the open end of the jar with its head or foot and accessing food from it.

Motivation to Feed from a Novel Object

I kept the budgerigars in the same cages as were used for the presentation of the Jar task for one more day before returning them to their group cages. As with the individual tasks, they were maintained in pairs until 1200 hours / 1230 hours, at which point a wooden board was used to separate them by dividing the cage in two, and they were food deprived for one hour. After this time, I set up a video camera and introduced a novel object – an egg cup (Fig. 4.2) – containing millet seeds, into each

individual's half-cage. A camera was set to record, and I left the room for two hours. If, after this time, neither bird appeared to have fed from its egg cup, I left them for a further two hours. If both had fed, I returned them to their group cage. (If one bird had fed and one had not, I left both birds *in situ* in order to minimise disturbance to the bird that had yet to feed, and for whom testing was not over). Water and perching material remained available to both birds throughout the food deprivation and testing period. At 1700 hours / 1730 hours, regardless of whether either bird had fed or not, I terminated the trial and returned them both to their group cage, where food was available *ad libitum* for at least one hour prior to lights being turned out.

The novel object itself consisted of a porcelain egg cup (5.5 cm H x 5 cm diameter) filled to within 0.5 cm of the rim of the cup with millet seed clusters.[3]

Figure 4.2: Novel object presented in boldness / exploration test.

[3] As with my individual problem solving ability test, I had originally intended to present birds with several different novel objects in order to obtain more generalisable estimates of their neophobia / aversion to explore and feed from or near novel objects. Unfortunately, since birds often exhibited some separation anxiety when housed alone, it was necessary for ethical reasons to restrict the number of novel objects they were presented with to one.

I watched videos back using Windows Media Player, and recorded how long it took each bird to approach and feed from the novel feeder, which I then used as a measure of individual neophobia / aversion to explore and feed from a novel object – the lower the score in seconds, the less neophobic the bird. Feeding was defined as per Brockway, 1964a ('the head is held close to food and directed at it. The beak need not necessarily be in contact with the food'). Birds that did not feed were assigned a ceiling value of 14,400 seconds (four hours).

Body Condition

Once all group foraging experiments were complete, I weighed all group members to the nearest 0.01 g. This was done by catching each bird individually and placing it gently inside a cloth drawstring bag, which was put in a plastic tub and then placed on an electronic balance located in the same room as the bird's cage.

To gain a measure of absolute body size, I then held each bird (keeping its head inside the dark cloth bag) and measured the tarsus length of its left leg using digital callipers. Two measurements to the nearest 0.1 mm were taken and averaged.

Combined, these measurements were used to estimate each budgerigar's nutritional state (relative 'fatness') as a proxy of its physiological state. Body condition was operationally defined as its residual on a regression of $\log_{10}$-transformed body mass versus $\log_{10}$-transformed tarsus size (Jakob *et al.*, 1996; see Boogert *et al.*, 2010 for an example of the method in use on Zenaida doves, *Zenaida aurita*).

Other Variables

Additional traits measured and included in the study were: each budgerigar's age in years, its sex, and the average length of time during group foraging presentations (seconds per trial) it spent (a) contacting tasks, and (b) scrounging food from already-solved tasks, prior to making its first task solve.

These last two potential predictors of a bird's propensity to exhibit food production behaviour may be somewhat restricted to the experimental paradigm used here, and rather less generalisable to other foraging contexts than character traits such as age or sex. The limitations of any conclusions that can be drawn based on these predictors will be highlighted in the discussion.

Demonstrators

I did not include in my analyses information relating to the competitive rank, individual learning ability, motivation to feed from a novel object, body condition, age, sex, or length of time spent interacting with or scrounging from tasks, of the birds I used as demonstrators. This was to avoid potentially skewing the results generated by my analyses of character traits (possibly) correlated with task solving / production behaviour. Several of my demonstrators came from a pool of birds that had had their behaviour shaped in order to turn them into competent task solvers prior to their insertion into one of my five test groups – and thus could not be considered innovators in their own right. The remainder were birds that had either innovated or acted as producers under their own volition in one test group before being 'seeded' into

another. However, individual-level data pertaining to these birds were already included in my analyses with respect to their own groups; therefore it would have been inappropriate to include them a second time.

Analyses

All analyses were carried out in R version 2.13.1 (R Development Core Team, 2011). Cox Proportional Hazards Models were run using the survival package (Therneau and Lumley, 2011).

Skill Pool Formation

To look for evidence of budgerigars developing skill pools, in which birds adopted producing (task solving) roles in some foraging situations but not others, I compared individuals' behaviour across each pair of foraging tasks (Tube/Flap; Tube/Lucky Dip; Tube/Drawers; Flap/Lucky Dip; Flap/Drawers; and Lucky Dip/Drawers), and recorded whether they had solved both tasks in a given pair, solved neither, or solved one but not the other. I then ran contingency (Fisher's Exact) tests to assess the degree of association between individuals' behaviour during presentations of each different pair of tasks.

If a disproportionate number of individual birds showed consistency in their behaviour across task pairs (solving both tasks or neither task), I interpreted this as a lack of evidence for the formation of skill pools – vice versa if birds frequently solved one member of a given task pair, but not the other.

I also fitted a Cox Proportional Hazards Model containing bird identity as a frailty (random) effect to test for a within-individual correlation in time to first solve each of the four different tasks presented to groups. A censoring indicator was applied to the model to take account of any birds that failed to solve tasks within the timeframe of trials 1-7.

Individual Characteristics

To investigate which, if any, of the individual character traits I measured were useful predictors of when, if at all, a bird would make its first solve of each of the four tasks that were presented during group trials, I fitted a number of Cox Proportional Hazards Models. Fixed effects included birds' age, sex, body condition, time taken to feed from a novel object, time spent contacting the asocial (Jar) task, success / failure at solving the asocial (Jar) task, competitive rank within their group, mean time per trial spent interacting with the Tube, Flap, Lucky Dip, and Drawers tasks, and mean time per trial spent scrounging from the Tube, Flap, Lucky Dip, and Drawers tasks. To allow for potential differences in birds' first solve times resulting from the somewhat different conditions under which each of the four group tasks were presented, I also included scrounge condition and demonstrator condition, as well as task identity (Tube, Flap, Lucky Dip, or Drawers), in the model as fixed effects. Bird was included as a frailty (random) effect. A censoring indicator was applied to the model to take account of any birds that failed to solve tasks within the timeframe of trials 1-7.

Rather than use a model-selection procedure to identify the best model, I used a model-averaging approach, based on Akaike's information criterion, corrected for

sample size (AICc) (Burnham and Anderson, 2002). A key advantage of model-averaging over the model-selection approach is that it is able to take into account uncertainty as to which model is best. AICc estimates the Kullback-Leibler (K-L) information for a model (the extent to which the predicted distribution for the dependent variable approximates its true distribution), and makes it possible to calculate an Akaike weight for each model giving the probability that the model in question is the actual best K-L model available, allowing for sampling variation. By summing the Akaike weights for all models that contain a particular variable, it is possible to obtain the probability that a variable occurs in the best K-L model, and therefore quantify the support provided by the data for an effect of a variable.

In this case, a very large number of individual models, based on every possible combination of variables (8192 in total), were fitted. It would have been impractical to take all of these into account in my calculation of the weights of individual variables and so I instead calculated the 'total' weight of each predictor based on its occurrence in those models that accounted for the first 90% of weightings (the top 152 models in my set of 8192), assuming that Akaike weights and estimates calculated over this 90% model set would closely approximate the unconditional estimates.

For every variable considered, its total Akaike weight and model-averaged estimate are given. Wald 95% confidence intervals were calculated using the unconditional standard error (Burnham and Anderson, 2002).

Results

Skill Pool Formation

A relatively high proportion of the birds in my study (12 out of 37) failed to act as producers during the presentation of any of my four foraging tasks. Some birds, by contrast, produced food from multiple different tasks types, with two birds solving all four tasks, and a further five birds each solving three tasks (Fig 4.3).

Across most task pairings, relatively more birds behaved in the same way during the presentation of two different foraging tasks (i.e., solved both tasks or solved neither task), than behaved differently (i.e., solved one task but not the other). This association reached significance in the Lucky Dip/Drawers pairing (p = 0.033), and was very close to significance in the Tube/Flap pairing (p = 0.052) (Table 4.1). Birds did sometimes solve one task and not the other, but only in the Flap/Drawers pairing, did more than half of the birds that solved one type of task, fail to solve the other.

In addition, a Cox Proportional Hazards Model containing bird identity as a frailty (random) effect revealed a significant correlation between individual birds' first task solve times across different tasks (Wald test: $\chi^2 = 46.6$, df = 24, p = 0.0035), i.e., some birds were consistently quick task solvers whereas others were consistently slow, or did not solve any tasks at all.

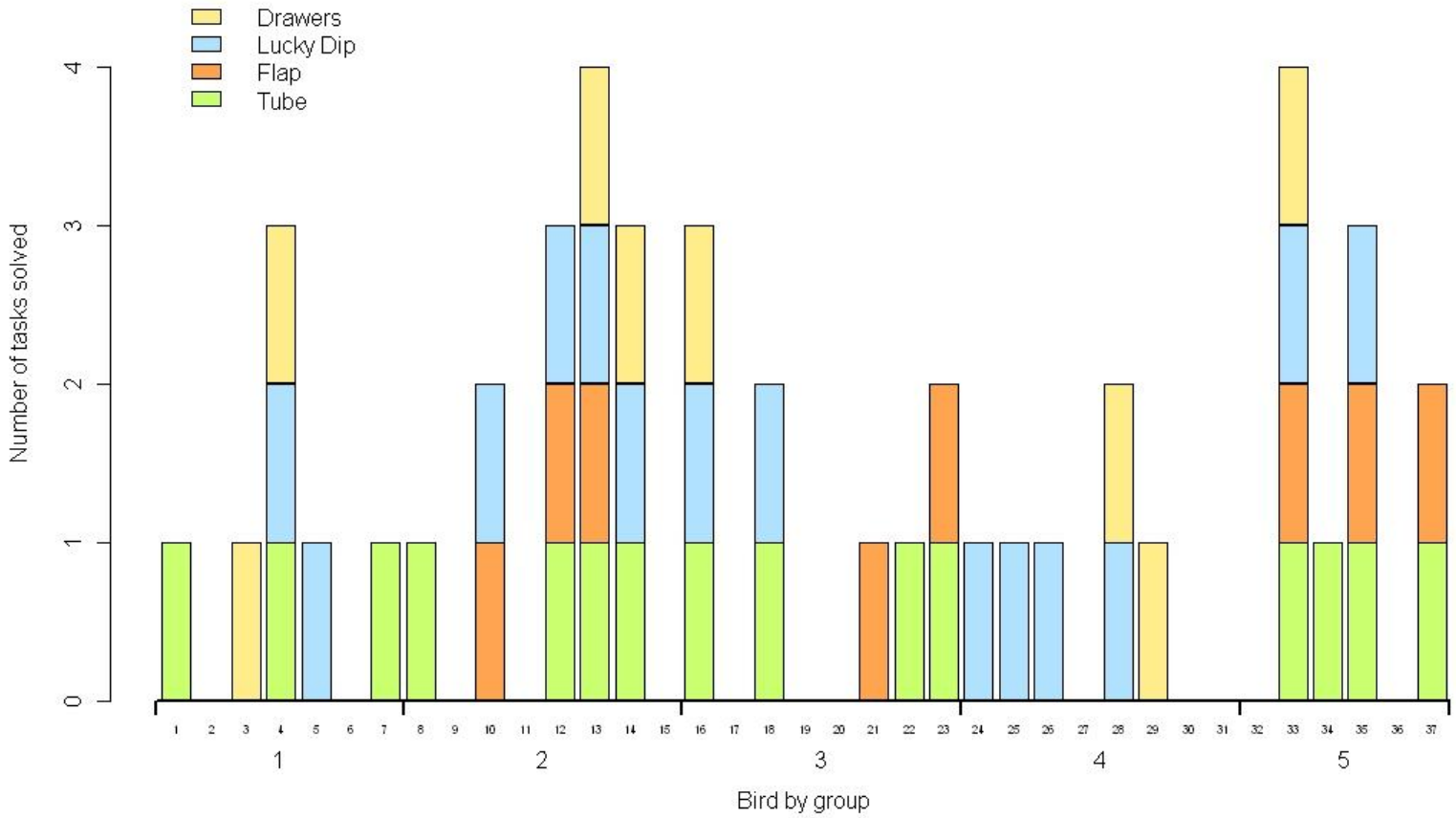


Figure 4.3: Total number of tasks solved by each bird, groups 1-5.

Table 4.1: Similarity in birds' behaviour ('solve' or 'not solve') across pairs of foraging tasks compared using Fisher's exact test. The odds ratio is (odds solved task 1|solved task 2)/(odds solved task 1|did not solve task 2). e.g., a bird that solved the Drawers task is estimated to have 7.58x greater odds of having solved the Lucky Dip, and vice versa.

Task	**Tube**	**Flap**	**Lucky Dip**	**Drawers**
Tube		Odds ratio = 5.68, 95% CI = [0.81, 68.68], ***p* = 0.052**	Odds ratio = 2.59, 95% CI = [0.54, 13.45] *p* = 0.19	Odds ratio = 3.04, 95% CI = [0.47, 24.27] *p* = 0.23
Flap			Odds ratio = 3.21, 95% CI = [0.50, 25.57], *p* = 0.22	Odds ratio = 1.39, 95% CI = [0.11, 11.64], *p* = 0.99
Lucky Dip				Odds ratio = 7.58, 95% CI = [1.04, 94.19], ***p* = 0.033**

Individual Characteristics

Cox Proportional Hazards Models produced strong support for two (competitive rank, and mean time spent contacting tasks per trial), and moderate support for another two (mean time spent scrounging from already-solved tasks per trial, and sex) of the individual-level characteristics I measured serving as useful predictors of how quickly an individual was likely to become a producer (i.e., there was a greater than 50% probability of each of these variables being present in the best K-L model) (Table 4.2).

Firstly, birds that spent relatively little time monopolising millet sprays when these were presented to their group (and that were potentially therefore of low competitive rank) were typically slower to act as producers for the first time when presented with the Tube, Flap, Lucky Dip and Drawers tasks than were birds that spent relatively longer monopolising millet sprays (and that were potentially therefore of high competitive rank). The estimated ratio for lowest / highest ranked birds was 0.1x, 95% CI = [0.07, 0.14] (Fig. 4.4).

Secondly, birds that spent proportionately longer scrounging from already-solved tasks during group trials also tended to be somewhat slower to solve tasks by themselves than were birds that engaged in relatively less scrounging, though support for this predictor was not as strong as that for rank. The estimated ratio for birds differing by one standard deviation in the amount of time they spent scrounging was 0.77x, 95% CI = [0.74, 0.79] (Fig. 4.5).

By contrast, birds that spent proportionately longer contacting tasks (whether or not these had yet been solved) during group trials, tended to make their first task solve more quickly than birds that spent only a little time contacting them. The estimated ratio for birds differing by one standard deviation in the amount of time they spent contacting tasks was 1.83x, 95% CI = [1.75, 1.91] (Fig. 4.6).

In addition, males were typically somewhat faster than females to make their first task solve, though support for this predictor was relatively weak. The estimated ratio for males / females was 1.79x, 95% CI = [1.58, 2.02] (Fig. 4.7).

There was little evidence that a bird's age, body condition, time to feed from a novel object, time spent contacting the asocial (Jar) task, or success / failure at solving the asocial (Jar) task, were good indicators of how quickly it would solve tasks when in a group (Table 4.2). Notably, though, bird identity remained an important predictor of an individual's time to first solve tasks, even when all other potential predictors had been taken into account (Wald test: $\chi^2 = 26.6$, df = 15, $p = 0.032$).

Table 4.2: Cox Proportional Hazards Model Individual-level predictor weights. 'Total support' is the total of the Akaike weights for models containing that variable, and gives the probability that the variable is in the best K-L model. Bold text indicates that a variable had support of 0.5 or above (>50% chance of being in the best K-L model).

	Age	**Sex**	**Body Condition**	**Novel Object Response**	**Asocial Task (Solve)**	**Asocial Task (Interact)**	**Competitive Rank**	**Contact Time (Group Tasks)**	**Scrounge Time (Group Tasks)**
Total Support	0.15	**0.53**	0.31	0.37	0.28	0.24	**0.99**	**0.99**	**0.61**
Model Average Coefficient (MAC)	-0.68	**0.58**	-4.69	0.40	-0.30	0.26	**-2.29**	**0.60**	**-0.26**
Unconditional SE	0.05	**0.06**	0.88	0.08	0.14	0.32	**0.16**	**0.02**	**0.02**
Back-transformed MAC	0.51	**1.79**	0.01	1.50	0.74	1.30	**0.10**	**1.83**	**0.77**
Wald Lower and Upper 95% CI	0.46, 0.56	**1.58, 2.02**	0.002, 0.05	1.29, 1.74	0.57, 0.97	0.69, 2.43	**0.07, 0.14**	**1.75, 1.91**	**0.74, 0.79**

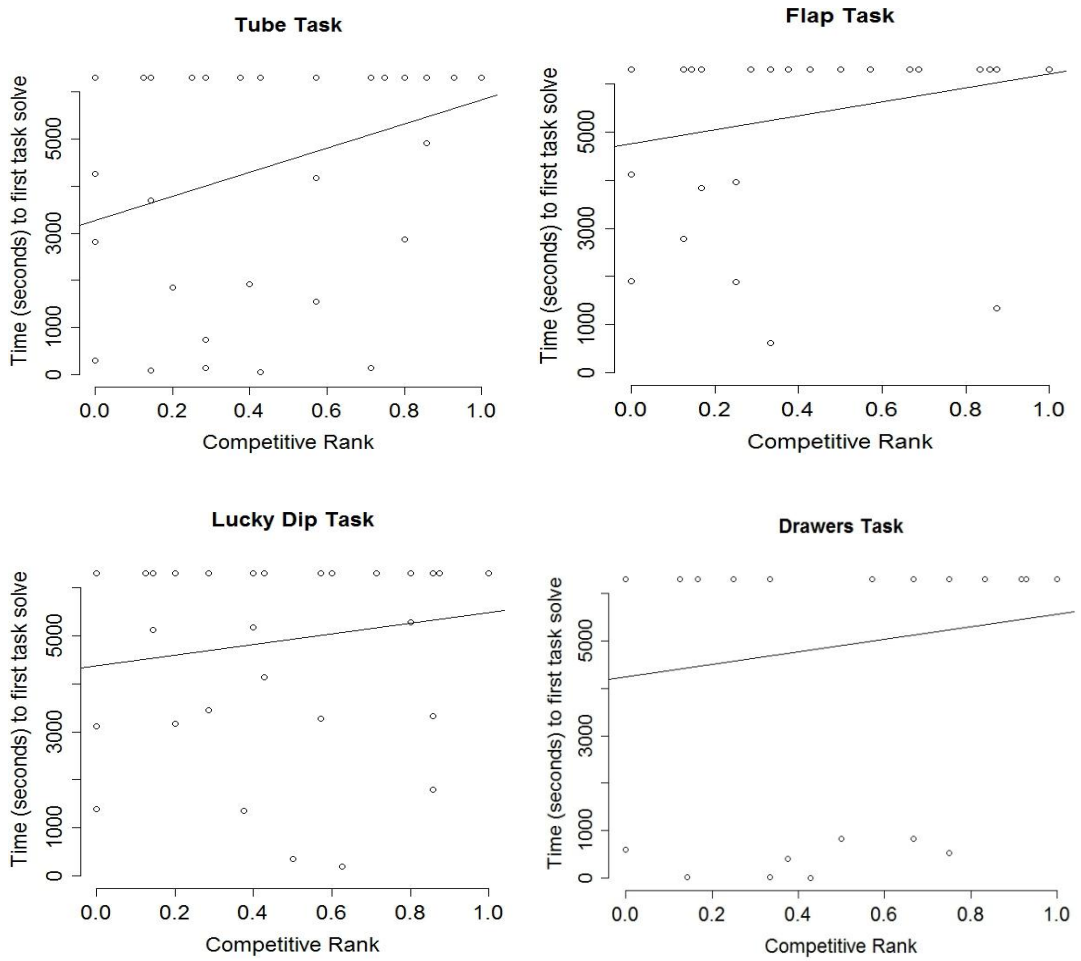


Figure 4.4: Birds' time to first solve each of four different tasks versus their competitive rank (0-1, highest – lowest ranked birds). For the purposes of graphical representation, birds that failed to solve tasks within seven 15 minute trials are here assigned a ceiling value 'solve time' of 6300 seconds.

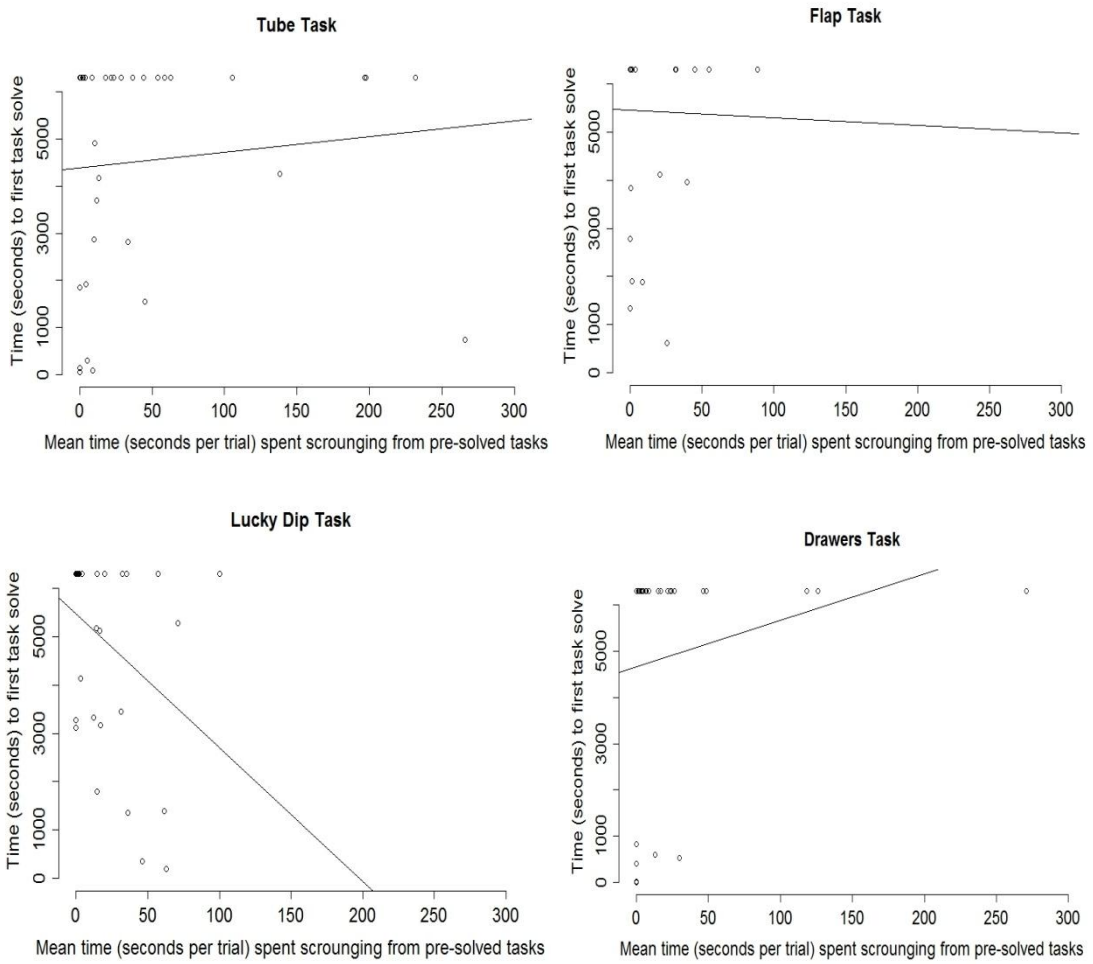


Figure 4.5: Birds' time to first solve each of four different tasks versus their mean time per trial spent scrounging from pre-solved tasks. For the purposes of graphical representation, birds that failed to solve tasks within seven 15 minute trials are here assigned a ceiling value 'solve time' of 6300 seconds.

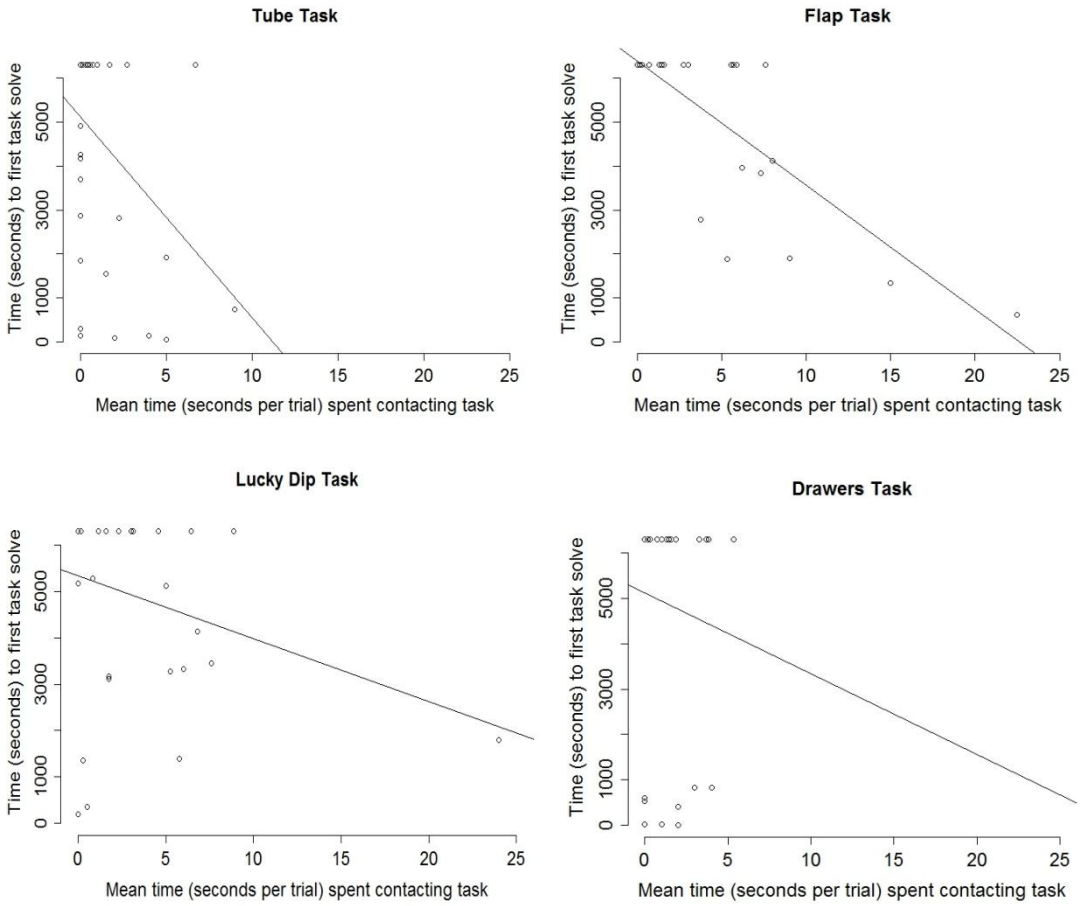


Figure 4.6: Birds' time to first solve each of four different tasks versus their mean time per trial spent contacting tasks. For the purposes of graphical representation, birds that failed to solve tasks within seven 15 minute trials are here assigned a ceiling value 'solve time' of 6300 seconds.

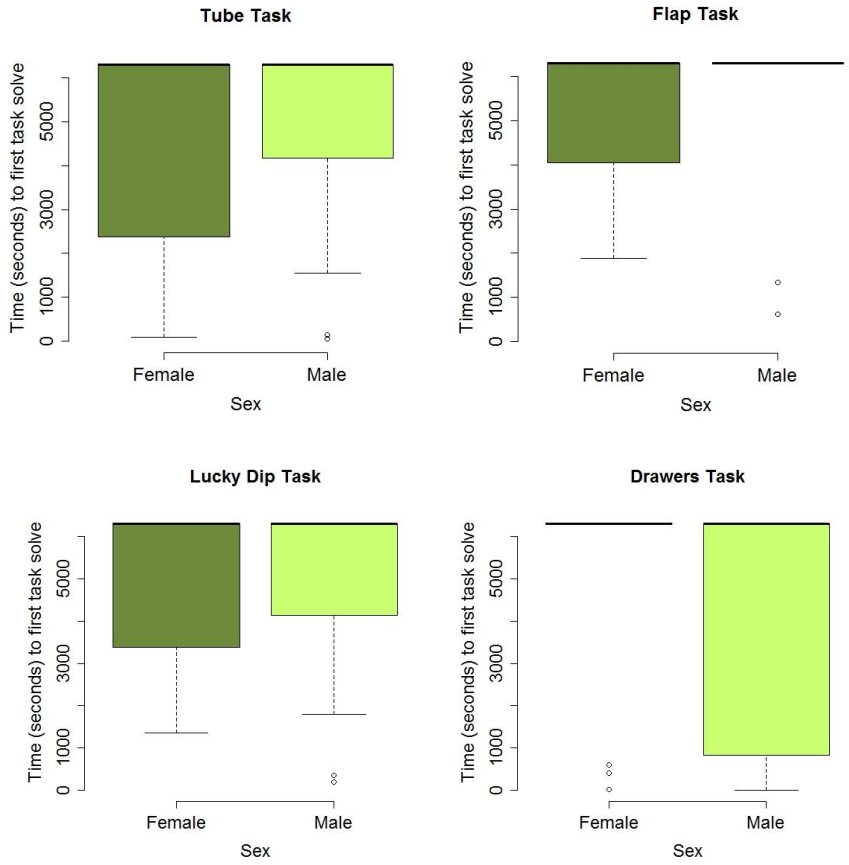


Figure 4.7: Birds' time to first solve each of four different tasks versus their sex. For the purposes of graphical representation, birds that failed to solve tasks within seven 15 minute trials are here assigned a ceiling value 'solve time' of 6300 seconds. (Bars denote the median number of solvers; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

Discussion

In this study, I assessed to what extent the same individual budgerigars operated as producers across the presentation of four different foraging tasks. The study also investigated which, if any, of a number of individual characteristics could be used as predictors of a bird's propensity to act as a producer.

Prediction 1

In accordance with my first prediction, I found evidence to suggest that certain individuals were disposed to operate as producers across a variety of foraging situations, whereas others exhibited little or no production behaviour under any circumstance. Though not completely clear cut, birds' behaviour tended to be reasonably consistent across tasks, with a greater proportion of individuals generally adopting the same behaviour for any given pair of tasks (solving both of them, or neither of them) than adopting different behaviour across them (solving one task, but not the other). Furthermore, birds also exhibited some consistency in their times to first solve different tasks, such that birds that were fast to solve one task, were typically also fast to solve other tasks.

Individuals did sometimes operate as producers in one foraging situation, and as scroungers in another, possibly offering some weak support for the skill pool hypothesis. However, such instances were comparatively rare, and may reflect differences in task difficulty (with some tasks, such as the Tube task, which was solved by 15 birds, possibly being easier to solve than others, such as the Drawers task, which was solved by only eight birds) as much as they provide evidence of a skill pool. This rarity, coupled with the fact that a large number of birds never once solved a single task of any type (Fig. 4.3), provided little indication that skill pools of individuals, each approximately equally adept at novel problem-solving, and each specialising in producing from a subset of task types, developed within groups.

Prediction 2

In accordance with my second prediction, I found that birds that acted as innovators and producers tended to share a number of characteristics: namely, their rank, length of time spent scrounging from foraging tasks prior to solving them for the first time, and length of time spent time contacting foraging tasks prior to solving them for the first time. There was also some evidence of a sex difference.

It is often assumed that the lowest ranking, least competitive members of a group ought to be its most innovative foragers (Reader and Laland, 2003). This is because innovation may be risky (and only worth attempting if an animal's current situation is unsatisfactory in some way – for instance, if it is failing to obtain sufficient food to meet its demands), and because, in circumstances where a producer-scrounger dynamic develops, dominant animals are usually expected to reap greater rewards from scrounging than subordinate ones (especially when food is clustered in patches from which dominants can displace subordinates, and then proceed to monopolise). In order to obtain any food at all, it may therefore be necessary for subordinate animals not only to act consistently as producers, but also to innovate new foraging methods (Barta and Giraldeau, 1998).

In this study, however, I found that 'low ranking' birds that spent relatively little time feeding from millet spray when this was provided to their group, tended to be somewhat slower to innovate or act as producers than 'higher ranking' birds that spent relatively longer feeding from millet spray (Fig. 4.4). I propose several possible reasons for this finding. Firstly, it is important to note that the budgerigars used in this

study were captive and well fed, and that no individuals may therefore have experienced any great 'necessity to innovate' in the space of my 15 minute foraging task presentations. It is possible that studies of wild budgerigars could yield very different results.

Secondly, although my measures of birds' 'competitive ranks' were intended to gauge individuals' ability to monopolise a food source (and do, to a certain extent, reflect this), it became apparent during data collection that, while some birds attempted to feed from the millet spray provided, but were quickly displaced by (presumably competitively superior) group mates, other birds appeared to take little or no interest in the food source and did not even attempt to approach it or feed from it. On the basis of how many seconds these birds spent feeding during millet spray presentations (none), they were classified as low ranking, when in reality it may have been that they were, for a variety of reasons, simply not motivated to feed from the millet sprays presented to them. Those same 'low ranking' birds that lacked the inclination to approach millet sprays during my assessments of competitive rank, may also have lacked the motivation to approach and interact with (millet-loaded) novel foraging tasks when these were presented to groups – leading to the appearance of 'low ranking' birds being slow to act as producers. Potential reasons for the disinclination of some budgerigars to approach and interact with both millet sprays and tasks could include lack of hunger, ill-health, and in some cases, reliance on mates for the provision of food (see later discussion on the influence of sex on birds' propensity to solve tasks). With hindsight, it might have been beneficial to assess birds' ranks using not just one, but several, forms of measurement. Boogert *et al.* (2006), for instance, measured 'agonistic rank' as well as 'competitive rank' in groups of captive starlings.

That said, since wild budgerigar flocks exhibit no obvious hierarchical structure (Wyndham, 1980), and the captive budgerigars in my study rarely exhibited any overt aggression towards one another, the ecological validity of attempting to attribute ranks on anything other than priority of access to food patches, is perhaps somewhat questionable.

Finally, it is worth noting that mine is not the first study to have found an apparently positive association between an animal's rank and problem solving proclivities (for example see Boogert *et al.*'s 2006 study on the spread of foraging innovations in groups of captive starlings). It is possible that, in some cases, individuals manage to obtain a high status precisely because of their innovativeness and cognitive abilities (Humphrey, 1976; Goodall, 1986; Chase et al, 2002; Thornton and Samson, 2012). For instance, Goodall (1986) reported that a young male chimpanzee, *Pan troglodytes*, was able to attain alpha status by virtue of innovative use of empty cans to augment his threat displays. In my own study, it is difficult to envisage how previous innovations could have equipped particular budgies to be better defenders of a monopolisable resource (millet spray) than others, but on the basis of my findings, this cannot be ruled out.

I further found some evidence to suggest that those birds that spent relatively less time scrounging from pre-solved tasks, tended to become producers more quickly than those that spent relatively more time scrounging (Fig. 4.5) – perhaps because they dedicated a relatively greater amount of their time to interacting with yet-to-be solved tasks, and were thus likely to discover how to solve them more rapidly. At first glance, this finding appears to contradict, somewhat, my earlier finding in Chapter

Three: that budgerigars were generally no faster to solve tasks for the first time in low-scrounge conditions than they were in high-scrounge conditions. The Cox Proportional Hazards Models fitted here, however, had already taken both scrounge condition and demonstrator condition into account as fixed effects. Thus, this latest finding relates primarily to individuals' behaviour relative to one another *within* a given scrounge and demonstrator condition.

In addition, my results indicated that birds that devoted a greater amount of time per trial to interacting with tasks were generally quicker to solve them for the first time, than were birds that spent only short periods of time manipulating them (Fig. 4.6). A key element, therefore, of being a successful producer of food from a new source, may be a motivation to engage with prospective new food supplies persistently. Birds that exhibited sustained interest in, and manipulated tasks for relatively lengthy periods of time during trials, appeared to have a greater chance of solving them (probably initially through trial and error) in a shorter overall time frame than did birds that engaged with them for only brief stints at a time.

It should be pointed out, however, that while the above two predictors (scrounge duration from, and contact duration with, tasks) of birds' propensity to act as producers when foraging in a group may be generalisable to other foraging contexts, their utility as predictors may in fact be limited to the experimental paradigm used here. Indeed, even here, although birds' time spent scrounging from already-solved tasks appeared in general to be negatively correlated with their time to first solve tasks by themselves, this relationship did not appear to hold true in the case of the Lucky Dip task. Further studies of the producer-scrounger game under a wider variety of

contexts (e.g., with a wider range of foraging problems; with more or less monopolisable food resources; or with more or less clumped food patches) will be needed to establish how well birds' inclination to act as scroungers, and their motivation to engage persistently with foraging problems, in fact serve as useful predictors of production activity.

Lastly, I also found some evidence that a bird's sex influenced its propensity to act as a producer, with male budgerigars overall being marginally quicker to solve tasks than females (although in most instances, sex differences in task solving time appeared to be small, with the apparent superiority of males stemming largely from their task solving activity when presented with the Drawers task) (Fig. 4.7). In the wild, males are known to feed their mates both during courtship (Brockway, 1964) and, later, when the female is incubating eggs and provisioning young in the nest (Radtke, 1988). Thus, in the grasslands of Australia, where food supplies are highly ephemeral, it is possible that male budgerigars may have evolved somewhat more flexible foraging strategies than females (potentially being relatively more willing to approach and interact with novel food types, or novel food patches) in order to obtain enough food to satisfy their own, their mates', and their offspring's energetic demands. Since there was relatively weak support for this particular predictor, however, and the number of birds used in the study was relatively small, it is also possible that any perceived sex differences in birds' tendencies to act as producers may have been due to sampling error.

Perhaps surprisingly, I failed to find any evidence that birds' task-contacting or task-solving performances under asocial conditions, were positively associated with their

propensity to solve tasks under group conditions. Nor did birds that were relatively fast to feed from a novel object (again, while being housed alone) appear to solve tasks at a significantly different rate than those that were slow to feed from it. However, collecting data from budgerigars housed on their own was difficult, with individual birds responding differently to being separated from the rest of their group. Some appeared to adjust rapidly, whereas others appeared to remain anxious throughout the testing period. Therefore, any measures of asocial learning ability or neophobia that I obtained are likely, at best, to provide only very crude indications of each bird's actual problem-solving ability and response to novel objects, and it would be inappropriate to make any firm inferences on the basis of these data.

It is also important to note that factors such as dominance, scrounging and social learning are all likely to influence individual birds' behaviour in social contexts, but will have no influence in an asocial context. In the case of some budgerigars, these social influences may have acted in combination with their underlying asocial ability / tendency to approach novel objects, to increase their propensity to solve tasks when foraging in a group. In the case of others, however, these social influences may have served to stifle birds' underlying disposition to solve tasks / approach novel objects. This, therefore, may be another reason for the lack of correlation detected in this study between birds' task solving abilities and reactions to a novel object when alone, and their propensity to solve tasks when in a group.

I also found little evidence of budgerigars' age or body condition being important indicators of how quickly they were likely to solve new tasks. All of the birds in my study were either late juveniles (approximately six months old) or relatively young

adults (one to two years old). It is possible that age differences in task solving ability, if they exist, may be easier to discern among birds that differ in age from one another to a greater extent than those observed here. Personal observations of newly fledged budgerigars during earlier experiments, for instance, suggested that young birds were more investigative towards new objects than were older birds – a trait that could have bearing on their tendency to adopt producing roles when foraging in a group. Equally, it is possible that, even if the juvenile birds in this study were initially somewhat more explorative of tasks than were the adults, they may have been relatively less skilled at actually manipulating them (similar to the juvenile meerkats in Thornton and Samson's 2012 study). Thus, differences in exploratiVeness among birds of different ages may have been counterbalanced by differences also in their task manipulating skill and/or persistence.

With regards to body condition, my results are consistent with those of other studies (e.g., Boogert *et al.*, 2010 (field tests on Zenaida doves); Morand-Ferron *et al*., 2011 (field and captive tests on great tits)), which have generally failed to detect a correlation between an animal's body condition and its likelihood of innovating. In the case of my study at least, it is possible that the captive, well-fed birds that were used were all in a similarly well-nourished condition, masking any underlying effect of body condition on the speed with which they might adopt production behaviour.

Interestingly, even when all other potential predictors of producing behaviour had been taken into account in my Cox Proportional Hazards Models, bird identity itself remained as an important predictor of an individual's time to first solve each of the four tasks presented during group foraging tests. It is possible that other personality

attributes not considered in this study, such as neophilia (attraction to novel stimuli – usually, unlike my novel object response test, measured in the absence of a food reward) might, if measured, go some way to explaining this remaining inter-individual variation. If measured more rigorously, birds' ascocial learning abilities and neophobia levels might also prove to be better indicators of production behaviour than has been found thus far in this study. It is also plausible that, rather than – or in addition to – simply reflecting covariance with state or other behavioural traits, variation in birds' time to first solve tasks may represent inherent individual differences in their propensity to forage innovatively / act as producers – a possibility that has also been suggested by Cole *et al.* (2011) in a study of variation in spontaneous problem-solving performance among wild great tits.

Conclusions

To date, few producer-scrounger studies have assessed individual animals' performances over the course of a series of different foraging problems. Testing for the existence of skill pools within groups has therefore been limited (Beauchamp, 2006). So, too, has been the exploration of individual-level characteristics that could potentially influence an animal's proclivity to adopt producing or scrounging roles when foraging in a group.

In this study, I have found that, when presented with a series of four different foraging tasks, individual birds within budgerigar groups show little evidence of developing skill pools. Rather, certain birds appear to possess greater motivation and / or ability to operate as producers across a range of different foraging scenarios, while others

appear to be more committed to scrounging. I have further found that a bird's competitive rank and sex, as well as its balance of time between contacting unsolved tasks and scrounging from pre-solved tasks, may serve as useful indicators of how quickly it is likely to first become a producer.

Further Work

I was unfortunately unable to investigate whether birds that acted as consistent, prolific producers, continuing to solve tasks on multiple occasions (as opposed to making just one or two sporadic solves before reverting back to scrounging) once they had acquired the necessary motor skills to enable them to do so, shared any additional unifying characteristics, and / or whether their adoption of these roles depended mainly on them being one of the first members of their group to successfully solve a task. I was unable to test this on account of the fact that only a small number of birds in my study became consistent producers (not enough to enable me to run *GLMMs* of the sort already run here to assess what, if any, characteristics this sub-set of birds shared). In future, however, such an avenue of research might help to throw further light on the producer-scrounger dynamics of group foraging animals.

Another direction for future research might be to examine animals' adoption of producer or scrounger roles under a more diverse set of foraging circumstances than were presented in this study. The four tasks used here were relatively similar and presumably required a similar set of explorative and motor skills in order to be solved. It is possible that skill pools, if and when they do arise, are more likely to occur when widely different behaviours are required in order for food to be exploited in different

situations, since a greater number of individuals in a group might then be likely to possess the necessary set of attributes to equip them to act as producers in at least some of the scenarios they encounter.

In addition to measuring a greater range of personality attributes, it might also be profitable to look for hormonal predictors of an individual's propensity to act as a producer. In a study of innovative behaviour in greylag geese, *Anser anser*, Pfeffer *et al.* (2002) found that birds acting as producers (lid removers) at a food dispenser tended to excrete higher levels of faecal corticosterone than did other members of their group that acted as scroungers. Corticosterone is released in stressful situations (von Holst, 1998), and there is some evidence that an individual's cognitive performance may be greatest when it is in an intermediary state of stress or arousal (Mendl, 1999). Thus, the most proficient problem solvers in a group may also be those with relatively elevated corticosterone levels – a potentially interesting avenue of future research that could be conducted with budgerigars as a means of furthering this study.

In the next chapter, however, I move away from studying the producer-scrounger game and instead begin to examine budgerigars' use of social learning strategies – specifically, 'copy / approach others when uncertain' strategies – when making decisions about when and where to forage.

CHAPTER FIVE

NOVEL FORAGING PATCH CHOICES IN CAPTIVE BUDGERIGAR GROUPS

Abstract

Group foragers such as budgerigars, *Melopsittacus undulatus*, may utilise social, as well as personal, information when selecting foraging locations. Which of these two sources of information they prefer to rely on may depend on a number of factors. These include any potential costs incurred through personal sampling of the environment (time wasted, increased exposure to predation), along with the relative accuracy of personal versus social information, and how recently the personal or social information was collected.

Here, I present several groups of 12-14 captive budgerigars with six pairs of visually distinct novel foraging patches and examine their foraging decisions in the presence or absence of prior personal information concerning one patch, as well as in the presence or absence of (sometimes conflicting) current social information about the opposite patch.

I find that, in the absence of prior personal information, birds appeared to exploit the social information provided by knowledgeable members of their group, and fed at the same patch as these birds before exploring the other available patch. When all members of a group possessed 'uniform' prior personal information about one foraging patch but lack any information about the other, I find that they usually visited this patch before exploring the other one. However, when a group's knowledge was 'split', with some birds possessing prior personal information about one patch, while others in the group possessed prior personal information about the other, I find that a smaller proportion of individuals (relative to when birds possessed uniform prior

personal information) visited the patch with which they were already familiar before visiting the alternative one. This suggests that birds may remain responsive to social information provided by the foraging activities of others, even when this conflicts with their own personal information.

I further find that over the course of patch presentations, any initial group-level preferences for one member of a pair of patches over the other were (a) weak from the outset and (b) diminished somewhat over time as birds explored the available alternative. Thus, I find little indication that budgerigars developed enduring foraging 'traditions'.

Introduction

As detailed in Chapter Two, Budgerigars, *Melopsittacus undulatus*, are social birds, living in flocks numbering anything from a few pairs of individuals to several thousand birds (Forshaw and Cooper, 1978) and performing most of their diurnal activities as part of a group (Wyndham, 1980). They are nomadic, with their movements being determined largely by the availability of food (spinifex, grass weeds and ripening wheat) and water (Forshaw and Cooper, 1978).

Being birds that travel in flocks from one food patch to another and frequently enter unknown habitats containing unknown resources, it is possible that budgerigars' foraging efficiency may be enhanced by paying attention to the activity of other birds in their flock, as has been found to be the case in several other species (e.g., cliff

swallows, *Petrochelidon pyrrhonota* (Brown, 1988); red-winged blackbirds, *Agelaius phoeniceus* (Avery, 1994)). Paying attention to others may help birds to learn about novel foods (e.g., red-winged blackbirds (Mason and Reidinger, 1981)), or how to deal with a new resource (observational learning); to discover the location of food (local enhancement) (e.g., great tits, *Parus major* (Krebs *et al*., 1972)); and to learn about the 'quality' of a particular patch ('public information') (Valone, 1989; for empirical evidence see work on nine-spined sticklebacks, *Pungitius pungitius* (Van Bergen *et al*., 2004) and minnows, *Phoxinus phoxinus* (Webster and Laland, 2008)).

That said, whilst likely to have access to (potentially useful) social information when foraging, budgerigars may also, on at least some occasions, possess a certain amount of personal information about the location, variability and quality of any given foraging patch. This might include prior knowledge (described variously as 'pre-harvest' or 'prior information' – Valone, 1991, 1992) garnered during earlier visits to the same patch, and/or 'harvest' or 'sample' information collected during a birds' current visit. Thus, budgerigars may sometimes be required to choose between conflicting personal and social information, for instance when selecting a foraging patch to exploit.

The objective of this study was to add to a growing body of work investigating animal social learning strategies (see Chapter One for full details). A study by Valone and Giraldeau (1993) found that budgerigars relied predominantly on personal, not social, information when choosing when to depart from foraging patches. To further explore if and when budgerigars make use of social information, here I attempted to

investigate their relative use of personal versus social information when arriving at foraging patches.

Theoretical analyses of social learning (Boyd and Richerson 1985, 1988; Laland *et al.*, 1996) generally assume that individuals will be more likely to rely on social information if they lack any personal information to guide their decision making, than if they possess some relevant prior knowledge – especially if personal information is 'costly' to acquire (Boyd and Richerson, 1985; Laland, 2004). European starlings, *Sturnus vulgaris*, for instance, have been found to use public information regarding the foraging successes and failures of others when accurate information about patch quality is difficult or costly to acquire via personal sampling (Templeton and Giraldeau, 1996). Similarly, naïve guppies, *Poecilia reticulata*, have been shown to adopt the same route to food sources taken by knowledgeable demonstrators, even when other more direct routes are available (Laland and Williams, 1997, 1998) – possibly because the protection gained through aggregating with other individuals generally outweighs the alternative gain of more rapid, unimpeded access to a food source that might be made possible by individual exploration and greater reliance on personal information.

When individuals possess, or are able to obtain, a certain amount of personal information, as well as social information (for instance, about the location or quality of a foraging patch), theoretical analyses generally assume that they will weight the two sources of information equally (Clark and Mangel, 1984; Valone and Giraldeau, 1993; Templeton and Giraldeau, 1995). There may be many situations, however, in which a forager might benefit from weighting personal information above social

information, or vice versa. For example, some theoretical models predict that individuals should favour social information over personal information when the latter is outdated and therefore potentially unreliable – unless the environment an animal is operating in is so highly changeable as to mean any social information available is also likely to be outdated, in which case it should ignore this and acquire fresh personal information through direct sampling of the environment (Boyd and Richerson, 1985, 1988; Feldman *et al*., 1996; Henrich and Boyd, 1998). Meanwhile, Giraldeau *et al.* (2002) and Bikchandani *et al.* (1992, 1998) propose that individuals may typically use social information in preference to personal information, since the accumulated knowledge of conspecifics constitutes a source of information that is potentially more reliable than the knowledge they are likely to gain through individual sampling of the environment. This proposal, however, overlooks the fact that (a) animals may lack the sensory or cognitive abilities needed to evaluate available social information accurately and thus act upon it appropriately or copy it faithfully (Hoppitt and Laland, 2013), or that (b) 'transmitters' of social information may engage in deceptive behaviour that renders the information they provide unreliable (e.g., ravens, *Corvus corax* (Bugnyar and Kotrschal, 2002b); grey squirrels, *Sciurus carolinensis* (Steele *et al*., 2008)).

To date, a number of studies involving fish and birds have found evidence to suggest that animals use personal information when this is reliable and up-to-date, but that they place more reliance on social information if their personal information is out-dated (e.g., Klopfer, 1959, 1961; Templeton and Giraldeau, 1996; Day *et al*., 2001; van Bergen *et al*., 2004; Webster and Laland, 2008). Rafacz and Templeton (2003), for example, found that captive starlings were capable of exploiting public

information when placed in an unpredictable environment in which personal information was impossible to collect, but in which informative 'demonstrator' birds were sometimes present. However, they required extensive experience with this unpredictable environment before they were willing to use social information over personal information. This suggested an initial preference for personal information, with the use of social information being something of a last resort (Laland, 2004; Hoppitt and Laland, 2013). Meanwhile, in a study using captive nutmeg mannikins, *Lonchura punctulata*, Rieucau and Giraldeau (2009) demonstrated that birds provided with sufficiently persuasive social information could be induced to reduce the weight of even highly reliable personal information and choose the foraging patch at which they had seen other birds feeding, even when in their own previous experience, this had been a low-yielding patch. The authors suggest their result may reflect the fact that, when animals are unable to collect up-to-date personal information by means of patch sampling, they may opt to rely on social information about current conditions in order to decrease uncertainty. Studies on fish have further shown that, when the use of prior personal information is costly, individuals may switch to relying on social cues instead (Kendal *et al*., 2004).

When animals use social information provided by other individuals, behavioural patterns or 'traditions' shared by members of a group can become established (Fragaszy and Perry, 2003). In the guppy studies already described (Laland and Williams, 1997, 1998), for example, foraging routes were found to persist even after all the original members of a swimming group had been replaced with different fish, possibly on account of the severe costs that fish might incur by leaving the safety of their group in order to learn alternative routes (Day *et al*., 2001). Among humans,

conformist social learning frequently leads to the maintenance of persistent, and sometimes quite arbitrary, traditions (Richerson and Boyd, 2005), whilst chimpanzees have also been shown to persistently perform the prevalent behaviour in their group, sometimes even after discovering equally profitable alternatives themselves (Whiten *et al*., 1999; Whiten, 2005; Bonnie *et al*., 2007).

When studying the foraging behaviour of wild meerkats, however, Thornton and Malapert (2009) found that, while the presence of trained demonstrators initially drew naïve individuals to feed near one member of a pair of artificial, arbitrary landmarks, this preference was not of long duration, and the same individuals soon (over the course of a few days) began to explore and feed at the second landmark, with the result that traditions degenerated. Far from promoting long-term adherence to the behaviour of the majority, initial social learning about one landmark appeared to increase individuals' subsequent exploration and learning of similar alternatives. In light of this finding, Thornton and Malapert (2009) suggested that, among non-primates at least, in situations where there are 'ample opportunities for individual learning at low cost...traditions will tend to die out.'

Here, I examined the behaviour of small groups of captive budgerigars when presented with a series of pairs of novel foraging patches. Each patch was visually distinct, but contained an equal amount of food and was functionally similar in terms of how birds were able to access food from it (see methods section for details), and positioned at opposite ends of a group's enclosure.

In the first series of tests (Condition 1), all, or in some cases, most, group members had no prior information relating to either foraging patch. In the latter cases, two members of the group were given prior exposure to one of the patches, and had prior personal information that this patch was profitable to forage at. Here, I predicted that:

1) Birds with no prior information regarding either foraging patch would be more likely, and quicker, to feed at a patch, when their group contained two 'demonstrators' that had prior information about one of the patches, than when their group was composed entirely of naïve individuals.
2) Furthermore, naïve birds would typically feed at the same patch as the two members of their group that had prior information about that patch (the demonstrators), before they fed at the patch that no members of their group had previously experienced.

In the second series of tests (Condition 2), all group members had prior personal information relating to one member of each pair of foraging patches. In some cases, all group members had prior information about the same patch. In others, two members of the group (the 'minority group') were given prior experience of the opposite patch to which the rest of their group (the 'majority group') were exposed. Here, I predicted that:

3) Birds would typically be faster to feed at the patch they had prior personal information about, than they were to feed at the patch they lacked prior personal information about (i.e., they would weight prior personal information of one patch above potentially risky personal exploration of a novel patch,

and/or potentially unreliable social information provided by other members of their group).

4) This preference for the familiar patch would, however, be less marked in groups with 'split' prior personal information than in groups with 'uniform' prior personal information (i.e., that at least some birds would be receptive to social information provided by other members of their group about the foraging patch they themselves lacked prior personal information about, and feed from it more rapidly than when no social information was available about this patch).
5) Furthermore, in the split condition, that any preference for the unfamiliar patch would be relatively more marked in the minority group than in the majority group (i.e., that a motivation to maintain close to the rest of their group might override these birds' preference for personal over social information).

Across both Condition 1 and Condition 2, I predicted that:

6) Individuals' initial patch preferences would become less marked across repeated trials, as they eventually discovered / explored the second, equally profitable, patch available a short distance away from the first.
7) Individuals' latency to feed at a patch for the first time would decrease across repeated trials, as birds' exposure to both patches increased (presumably leading to a decrease in neophobia and a concurrent rise in competition for access to food at the patches).

Methods

Birds and Housing

Experiments took place in the St Andrews University bird unit, and used three groups of 12-14 mixed sex, mixed age, individually identifiable budgerigars. Approximately half the budgerigars had been purchased from local breeders and were approximately two years old. The remainder were bred in the St Andrews University bird unit, and were approximately one year old. Each bird was fitted with a Budgerigar Society leg ring for identification. Groups were composed in such a way that the birds could be distinguished by their plumage, since rings were not always readily visible.

Groups were housed indoors in a custom-built bird facility and kept in two rooms in miniature aviaries of size 81 cm W x 162 cm L x 173 cm H. Rooms were air conditioned at a temperature of 20-22°C and maintained on a light/dark cycle of 12/12 hours. Since birds were most motivated to feed close to the end of each day, 'sunset' time in the rooms was staggered by half an hour (1800 hours in one room and 1830 hours in the other) to allow experiments to be run in both rooms on the same day. For further details on housing conditions, see Chapter Two.

Design

I presented groups with up to six pairs of artificial foraging patches. Each pair consisted of two visually distinct yet similarly shaped and sized objects that could be accessed in similar ways to one another (e.g., from the aviary floor, by climbing down

from a perch, or by flying up and perching on the object itself), and were positioned at opposite ends of a group's cage (approximately 150 cm apart). Each object was loaded with a total of half a millet spray as a food reward. The first three pairs of patches (Condition 1) were presented to three budgerigar groups. The second three pairs (Condition 2) could unfortunately only be presented to two of these groups, on account of time constraints and the temporary ill health of several members of the remaining group.

Under Condition 1, all three groups were presented with some pairs of patches in the company of trained pairs of demonstrator birds that had already been exposed to, and knew how to feed from, one patch in a given pair; and with some pairs of patches in the absence of any demonstrators. (Demonstrators were pre-existing members of each group, which had been temporarily separated from the rest of the group during their pre-exposure to a particular patch – see later section on pre-training.) Presentations with and without demonstrators were counterbalanced across groups to ensure that all sets of foraging patches were presented to at least one group in the presence of demonstrators, and to at least one group in the absence of demonstrators. With the exception of demonstrators, all group members were completely naïve and had no previous exposure to either foraging patch prior to the beginning of experimental trials. Each pair of patches was presented to one group with no demonstrators; to one group, with demonstrators trained to feed from patch '*a'*; and to one group, with demonstrators trained to feed from patch '*b'* (Table 5.1).

Under Condition 2, by contrast, all group members were given access and exposure to one patch in a given pair prior to the beginning of experimental trials. In some cases,

all group members were given prior access to the same patch, whereas in others, although most group members (the majority group) were given prior access to the same patch, two birds (the minority group) were given prior access to the opposite patch. Each pair of patches was presented to one group with uniform prior knowledge, and to one group with split prior knowledge. In the first case, all birds were given prior exposure to patch '*a*'. In the second case, the majority of the group were given prior exposure to patch '*a*', whilst two birds were given prior exposure to patch '*b*' (Table 5.1).

Table 5.1: Foraging patch presentations across groups. D, 'Demonstrators'; ND, 'No Demonstrators'; G, 'Majority Group'; g, 'Minority Group'; a, b, patch to which birds were pre-exposed.

Patch Pairs	**Group 1**	**Group 2**	**Group 3**
	Condition 1		
Umbrellas	*D, a*	*D, b*	*ND*
Hangers	*ND*	*D, a*	*D, b*
Side Feeders	*D, a*	*ND*	*D, b*
	Condition 2		
Baskets	*G, a*	Did not participate	*G, a* *G, b*
Cubes	*G, a*	Did not participate	*G, a* *g, b*
Boxes	*G, a* *G, b*	Did not participate	*G, a*

Foraging Patches

Condition 1

i. Umbrellas

These were two modified hanging bird feeders comprising a feeding dish at the base, and an umbrella-like hood that could be raised or lowered along a metal post protruding from the centre of the basal dish. Base diameter was 21 cm, hood diameter was 30 cm. During trials, the hood was raised to a height of 15 cm, giving birds plenty of room to access millet spray located in the 4cm deep food dish underneath it. Hoods were covered in visually distinctive cardboard (patch '*a'*, yellow with green pipe cleaners, patch '*b'*, green with yellow and orange felt pompoms) (Fig. 5.1). During trials, patches were situated at the corners of opposite ends of a cage, on the floor.

ii. Hangers

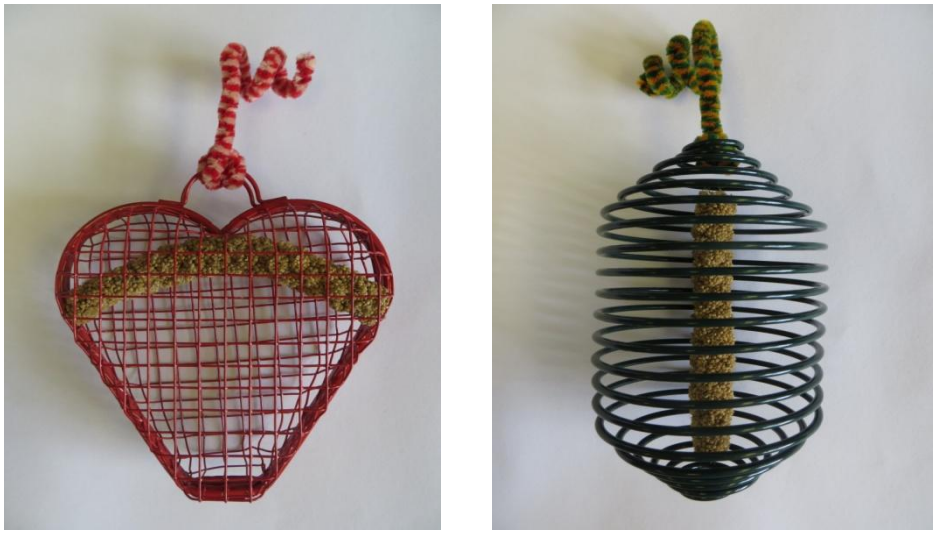
These were also made from two hanging bird feeders of approximately the same size, but different shapes and colours. Patch '*a'* was red and heart-shaped (13 cm H x 12 cm L x 4 cm W), patch '*b'* was green and cylindrical (15 cm L x 8 cm diameter). Pieces of millet were inserted inside the feeders, and were accessible to birds through gaps in their wire mesh (Fig. 5.1). During trials, feeders were positioned at opposite ends of cages at a height of approximately 1 m, suspended underneath perches that were already present in the cage and secured in place with pipe cleaners.

iii. Side Feeders

Again, these were modified hanging bird feeders of similar size, but different shapes and colours. Patch '*a'* was a green wire box (12 cm H x 13 cm L x 4 cm W) fronted with purple cardboard and pipe cleaners, patch '*b'* was a an artificial sunflower, disc-shaped (23 cm diameter x 4 cm deep) and fronted with yellow cardboard, yellow feathers and blue plastic oval shapes (Fig. 5.1). During trials, the feeders were fixed to opposite ends of the cage at a height of approximately 1 m, fastened to the cage bars with pipe cleaners.

(*i*)

(*ii*)



(*iii*)

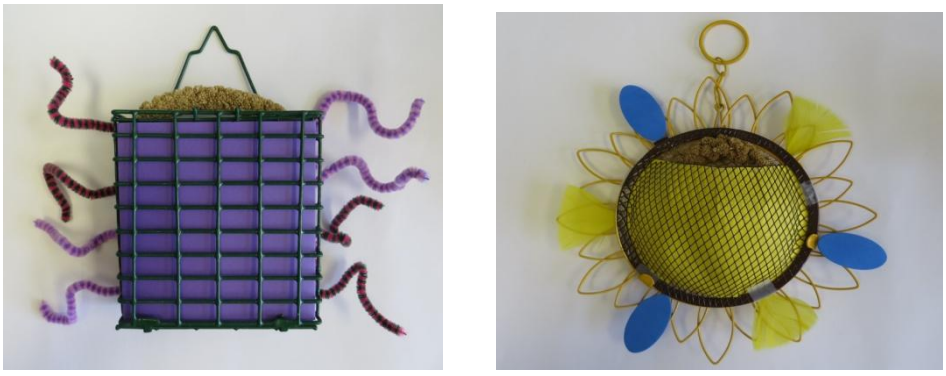


Figure 5.1: (i) Umbrella patches, (ii) Hanger patches, and (iii) Side Feeder patches. In each pair, patch 'a' is on the left and patch 'b' is on the right.

Condition 2

i. Baskets

These patches were each made up of three plastic flower pots (24 cm L x 7 cm W x 7 cm H), joined together in a row and covered with distinctively coloured and patterned paper (patch '*a'*, orange and black stripes, patch '*b'*, green squares). Pieces of millet spray were presented inside each flower pot, taped to cardboard bases secured 2 cm below the top of the pot (Fig. 5.2). During trials, patches were hung at opposite ends of the cage at a height of approximately 1 m, tied to cage bars using pipe cleaners.

ii. Cubes

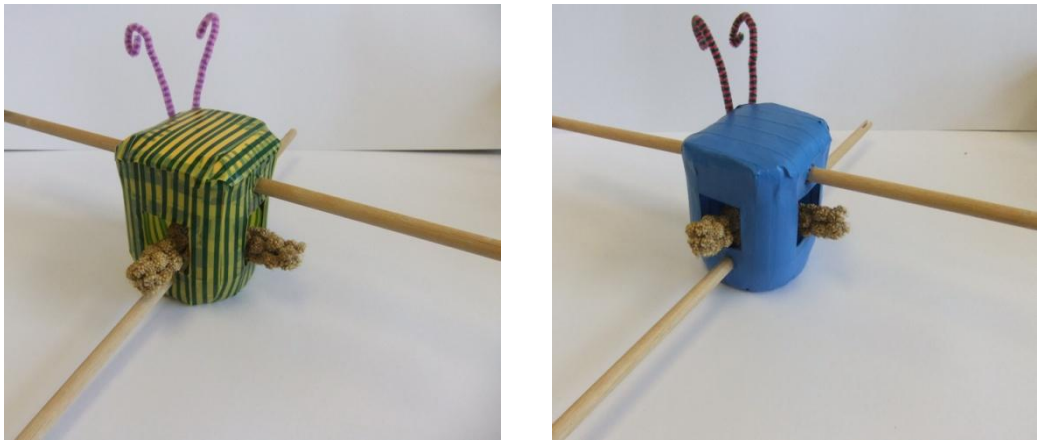
These patches were made from the base of a plastic water bottle (10 cm H x 8 cm L x 8 cm W), into which 3 x 3 cm feeding apertures had been cut on two sides of the bottle. These apertures were accessible via four wooden perches inserted through the sides of the bottle (0.5 cm diameter, approximately 15 cm L). Bottles were covered in distinctively coloured electrical tape (patch '*a'*, green/yellow stripes, patch '*b'*, blue), and pieces of millet spray were inserted through the apertures and secured inside the bottles using twine (Fig. 5.2). During trials, the cubes were positioned inside corners at opposite ends of the cage at a height of approximately 1 m, held in place using pipe cleaners and the support of two of the wooden perches, which were pushed in between the cage bars.

iii. Boxes

These patches were made from the middle portion of a plastic water bottle (13 cm L x 8 cm H x 8 cm W), and open at both ends. Four wooden perches (0.5 cm diameter, approximately 10 cm L) protruded diagonally out from each bottom corner of the hollow box. Bottles were covered in visually distinctive crêpe paper (patch '*a'*, green, patch '*b'*, red). A piece of millet spray was secured inside the box using twine, with its ends protruding from either end of the box (Fig. 5.2). During trials, boxes were positioned at opposite ends of cages at a height of approximately 1 m, suspended underneath perches that were already present in the cage and secured using pipe cleaners.

(*i*)

(*ii*)



(*iii*)

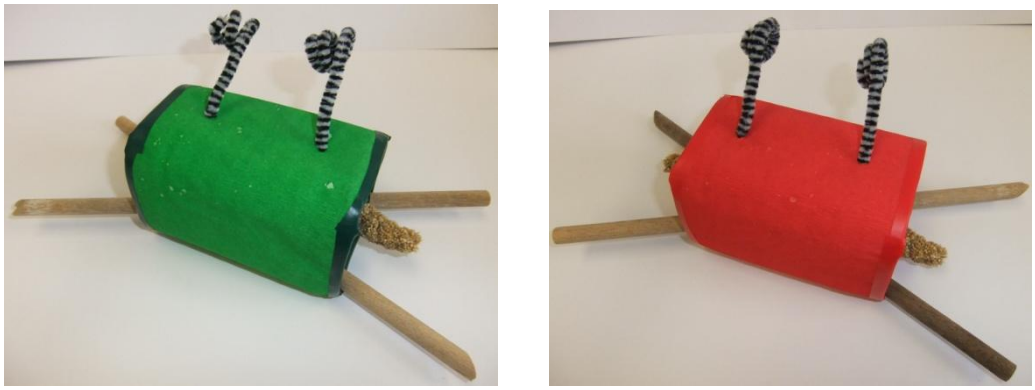


Figure 5.2: (i) Basket patches, (ii) Cube patches, and (iii) Box patches. In each pair, patch 'a' is on the left and patch 'b' is on the right.

Pre-Training: Condition 1

Pairs of birds from each group were chosen as demonstrators. The same pair acted as a group's demonstrators for both sets of trials in which demonstrators were required. Pairs were not randomly assembled, but selected on the basis of known association

preferences. Budgerigars are a highly pair-bonded species, and can exhibit considerable separation anxiety if housed alone or separated from their mate. Therefore, to minimise the likelihood of this being a problem during training (when it was necessary to physically and visually separate demonstrators from the rest of their group), as well as to speed up the training process by ensuring birds remained calm and willing to forage and explore new objects, I selected not simply pairs, but mated pairs, of birds to be demonstrators.

In order for training to begin, demonstrators needed to be separated from the rest of their group. This was done by ushering the pair into one half of their cage and retaining all other birds in the remaining half of the cage using an opaque divider. Following one hour of food deprivation (water remained available throughout), the required foraging patch was then presented to the pair, in exactly the same location, and containing the same type of food (half a millet spray), as would be presented in subsequent trials. A video camera was set up and left trained on the foraging patch for a maximum of three hours (1300-1600 hours / 1330-1630 hours) – less if the pair had clearly eaten several clusters of millet seeds within the first one or two hours of the session. During training, I left the room but made hourly checks to see if the patch had been eaten from. At the end of the training session, I removed the foraging patch from the cage, followed by the divider, so that all birds once again had access to the entire cage for the remainder of the day. Care was taken to ensure that the patch remained out of sight of the naïve birds behind the opaque divider whilst it was placed in, and taken out of the demonstrator's half of the cage. The same process was repeated daily, until such a time as at least one member of the demonstrator pair was seen to have fed from the patch on at least two different training sessions, for a total time of at least

120 seconds (usually much longer). Pairs required no more than three such training sessions in order to reach this criterion. Once they had reached it, and were feeding reliably, and for reasonable bouts of time, from their designated patch, group trials were begun the following day.

Pre-Training: Condition 2

To provide all members of a group with uniform prior knowledge of a particular patch, birds were food deprived for one hour (water remained available throughout) and then given access to a foraging patch for at least two one-hour periods (at 1300-1400 hours / 1330-1430 hours) on consecutive days directly preceding the day of the first proper trial. During this time, the patch was presented in exactly the same location, and containing the same type of food (half a millet spray), as during actual trials. A video camera was set up and left trained on the foraging patch during each session. Birds were deemed habituated to a patch when at least half of all members of the group had fed from the patch on at least two different days, each for a total time of at least 30 seconds. (Note that the criterion feeding duration for individual birds was lower here than during training sessions involving only two birds. This was because competition for access to foraging patches was considerably greater in larger groups of birds, and some birds, although showing sustained interest in a foraging patch, and having clearly formed an association between the patch and food, were unable to monopolise it for such lengthy periods of time as was possible during pair-training sessions.) In all cases, groups reached habituation criterion within two training sessions.

To provide groups with split prior knowledge, following one hour of food deprivation (water remained available throughout), two highly bonded birds were separated from the rest of their group, confined temporarily to one side of their cage and trained to feed at a particular foraging patch using the same methods as described above for demonstrator training during Condition 1 (i.e., given up to three training sessions, each of up to three hours long, at 1300-1600 hours / 1330-1630 hours). In the meantime, the remainder of the group, confined to the other side of their cage during this time, were food deprived for one hour (water remained available throughout) and given access to the opposite foraging patch in the pair, at which they were trained to feed using the same methods as described above for birds in the uniform prior knowledge condition in Condition 2 (i.e., given at least two one-hour periods at 1300-1400 hours / 1330-1430 hours on consecutive days directly preceding the day of the first proper trial, in which to feed at the patch). Thus, the two fractions of the group were trained concurrently, and in visual isolation from one another. Care was taken to ensure that patch '*a*' remained out of sight of those birds in the minority group, and patch '*b*' remained out of sight of those birds in the minority group, when the patches were inserted into and removed from groups' cages during these periods of pre-training.

Note that pairs of birds were given a longer period of time to learn to forage from their novel foraging patches (up to nine hours) than the rest of the group were given to learn to forage from theirs (as little as two hours). This was because previous pilot studies with the birds had shown them to be much slower to forage when housed in smaller numbers than when kept as a large group. Thus, birds housed in pairs

generally required, and were permitted, more time to approach and feed from their novel foraging patches than were birds housed in larger numbers.

Experimental Procedure

Birds were food deprived for one hour before trials began (water remained available throughout the food deprivation and testing period). During trials, each budgerigar group was given one pair of foraging patches with which to interact (Fig. 5.3). Prior to the insertion of the patches into their cage, all group members were ushered into the central portion of their cage by two experimenters (me and a helper) and retained there by two opaque dividers inserted from front to back through the cage. Each experimenter then placed one foraging patch at each end of the cage, in equally visible and accessible locations. A Canon HG10 high definition video camera was trained on each patch, and after inserting the foraging patches, the two experimenters turned these on and then, at the same time as one another, each pulled out one of the dividers behind which the group were being held, freeing birds to interact with both foraging patches. All activity around the two patches was then recorded for one hour.

Each pair of foraging patches was presented to each group a total of three times (once a day over three consecutive days), for one hour at a time. Trials were always conducted in the afternoon, when birds were most motivated to feed, beginning at 1600 hours or 1630 hours depending on which room they were housed in. At the end of a trial, both foraging patches were removed from the cage and food bowls returned, giving birds one hour, should they need it, in which to feed *ad libitum* before lights were switched off. Groups were always given a resting period of at least one week

between the completion of one set of trials and the beginning of a new round of pre-training (where necessary) and testing with a new pair of foraging patches.

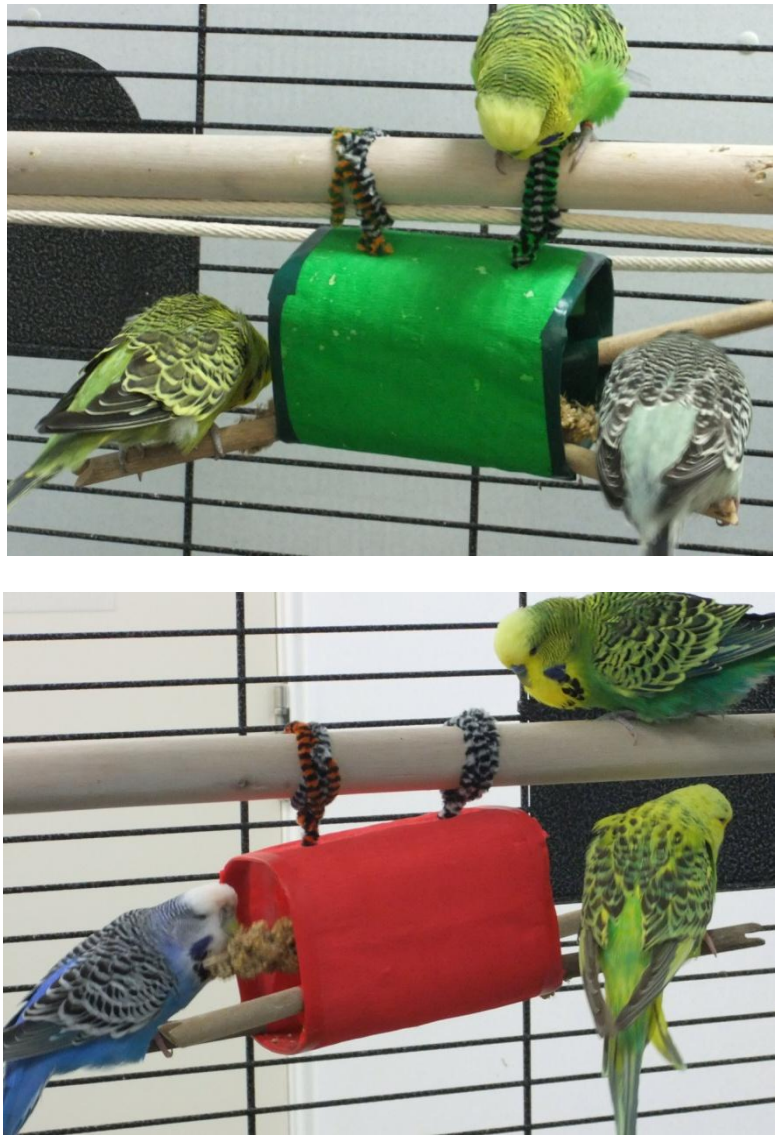


Figure 5.3: Patches 'a' and 'b' presented at opposite ends of a group's cage during a test trial (Box patches pictured).

Video Analysis

I watched videos using Windows Media Player, and for every trial, with every set of foraging patches, recorded the times at which each bird first fed at each of the two

patches in their cage. Feeding was defined as per Brockway, 1964a ('the head is held close to food and directed at it. The beak need not necessarily be in contact with the food').

Analyses

All analyses were carried out in R version 2.13.1 (R Development Core Team, 2011). Cox Proportional Hazards Models were run using the survival package (Therneau & Lumley, 2011), and Generalised Linear Mixed Models (*GLMMs*) were run using the lme4 package (Bates *et al*., 2011).

Condition 1

Time to First Feed at a Patch (All Groups)

I fitted a Cox Proportional Hazards Model to assess birds' time to first feed at either one of the two presented foraging patches. Demonstrator condition (present / not present) was included as a fixed effect and trial as a covariate, plus the interaction between them. The pair of patches (Umbrellas, Hangers, or Side Feeders) that was being presented was included as a further fixed effect, and bird identity was included as a frailty (random) effect. First feeding times of demonstrators themselves, when present, were not included in the model. A censoring indicator was applied to take account of any birds that failed to feed at either patch during a trial. Effect sizes and confidence intervals are reported on the back-transformed multiplicative scale.

Proportion of Group to Feed at a Patch (All Groups)

To analyse whether the proportion of group members that fed at either one of the two patches presented, differed according to whether or not their group contained demonstrators, I used a *GLMM* with a binomial error distribution and logit link function. Data were checked for overdispersion prior to running the model. Demonstrator condition (present / not present) was included as a fixed effect and trial as a covariate, plus the interaction between them. Patch pair type (Umbrellas, Hangers, or Side Feeders) was also included as a fixed effect, and group and bird were treated as nested random effects. Effect sizes and confidence intervals are reported on the back-transformed odds ratio scale.

Proportion of Group to Feed First at the Demonstrated Patch versus the Non-demonstrated Patch (Demonstrator-containing Groups Only)

To analyse the proportion of group members that fed first at the patch the demonstrators in their group had been trained to feed at (the demonstrated patch), relative to those that fed first at the opposite patch (the non-demonstrated patch), I used a *GLMM* with a binomial error distribution and logit link function. Data were checked for overdispersion prior to running the model. Patch (demonstrated / non-demonstrated) was included as a fixed effect and trial as a covariate, plus the interaction between them. Patch pair type (Umbrellas, Hangers, or Side Feeders) was also included as a fixed effect, and group and bird were treated as nested random effects. Effect sizes and confidence intervals are reported on the back-transformed odds ratio scale.

Condition 2

Time to First Feed at Familiar / Unfamiliar Patch (All Groups)

I fitted a Cox Proportional Hazards Models to assess birds' time to first feed at the foraging patch (in each pair of foraging patches presented) to which they had been exposed during pre-training, and with which they were therefore already familiar. For the majority of group members, patch '*a'* was the familiar patch, though for pairs of birds in some groups, patch '*b'* was the familiar patch. I then fitted a second model, identical to the first except excluding, where present, the two birds in each group that were familiar with patch '*b*'. Note that, ideally, I would also have fitted a third model, this time including these two birds and excluding those that were familiar with patch '*a*', but there were insufficient data for this model to be fitted.

I also fitted Cox Proportional Hazards Model to assess birds' time to first feed at the foraging patch (in each pair of foraging patches presented) to which they had *not* been exposed during pre-training, and with which they were *not* already familiar. For the majority of group members, patch '*b'* was the unfamiliar patch, whereas for pairs of birds in some groups, patch '*a'* was the unfamiliar patch. I then fitted a second model, identical to the first except excluding, where present, the two birds that were unfamiliar with patch '*a*'. Again, ideally, I would also have fitted a third model, this time including these two birds and excluding those that were unfamiliar with patch '*b*', but there were insufficient data for this model to be fitted.

In all models, groups' prior knowledge state (uniform – all birds with previous exposure to patch '*a*', or split – most birds with previous exposure to patch '*a*', two with previous exposure to patch '*b*') was included as a fixed effect and trial as a covariate, along with the interaction between them. The pair of patches (Baskets, Cubes, or Boxes) that was being presented was also included as a fixed effect, and bird identity was included as a frailty (random) effect. A censoring indicator was applied to take account of any birds that failed to feed at either patch during a trial. Effect sizes and confidence intervals are reported on the back-transformed multiplicative scale.

Proportion of Group to Feed First at Familiar / Unfamiliar Patch (All Groups)

To assess what proportion of group members fed first at the patch with which they were already familiar (as opposed to feeding first at the patch with which they were unfamiliar, or not feeding at either patch), depending on whether their prior knowledge was uniform or split, I used two *GLMMs* with a binomial error distribution and logit link function. Data were checked for overdispersion prior to running the models. In both models, groups' prior knowledge state (uniform or split) was included as a fixed effect and trial as a covariate, plus the interaction between them. Patch pair type (Baskets, Cubes, or Boxes) was also included as a fixed effect, and group and bird were treated as nested random effects. Effect sizes and confidence intervals are reported on the back-transformed odds ratio scale.

In the first model, all group members were included. In the second model, however, the two birds from the minority group (birds familiar with patch '*b*') in the split

condition were excluded. Note that, ideally, I would also have fitted a third model including the two birds from the minority group and excluding those in the majority group (birds familiar with patch '*a*'), but there were insufficient data for this model to be fitted.

I then ran a second pair of models, identical to the two describe above, but this time assessing what proportion of group members fed first at the patch with which they were unfamiliar (as opposed to feeding first at the patch with which they were already familiar, or not feeding at either patch), depending on whether their prior knowledge was uniform or split.

Results

Condition 1

During the first presentation of novel foraging patches in demonstrator-present conditions, all demonstrators that visited a patch fed at the one they had been pre-habituated to, before they fed at the patch with which they were unfamiliar. Moreover, in four out of six cases, one member of each demonstrator pair was the first bird in each group to feed at the relevant patch, thus potentially providing social information to the naïve members of its group. In a fifth case, a demonstrator was the second bird in the group to feed at the patch it had been pre-habituated to (approximately five seconds after one previously naïve member of its group). All five of these cases were included in analyses. In a sixth case (Group 1, Umbrella patches), however, neither

bird in the demonstrator pair fed at either the umbrella patch to which they had been pre-habituated, or the umbrella patch to which they had not been pre-habituated, over the course of trials 1-3. This final case was excluded from analyses.

Time to First Feed at a Patch (All Groups)

A Cox Proportional Hazards Model showed no significant interaction between demonstrator condition (present / not present) and trial (Wald test: $\chi^2 = 0.25$, df =1, $p = 0.61$, 95% CI = [0.60, 1.35]) in birds' time to first feed at a patch. Upon removing the interaction term, there was no evidence of a difference between demonstrator conditions (Wald test: $\chi^2 < 0.06$, df =1, $p = 0.81$), with birds first feeding at patches 0.95x as quickly when demonstrators were present in their group than when they were absent (95% CI = [0.65, 1.40]) (Fig. 5.4). There was, however, a significant difference in how quickly birds first fed at patches as trials progressed (Wald test: $\chi^2 = 23.41$ df =1, $p < 0.001$), with birds in trial 3 typically feeding at patches 2.80x more quickly than birds in trial 1 (95% CI = [2.28, 3.45]) (Fig. 5.5).

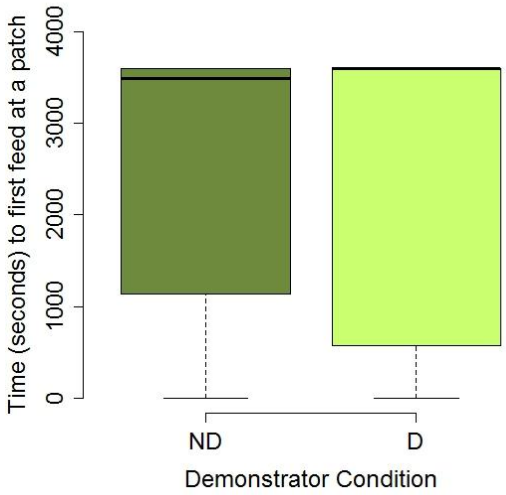


Figure 5.4: Birds' time to first feed at a foraging patch in a given trial under no demonstrator present (ND) versus demonstrator present (D) conditions. For graphical representation, birds that failed to feed at either patch are here assigned a ceiling value 'feed time' of 3600 seconds. (Bars denote the median time to first forage; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

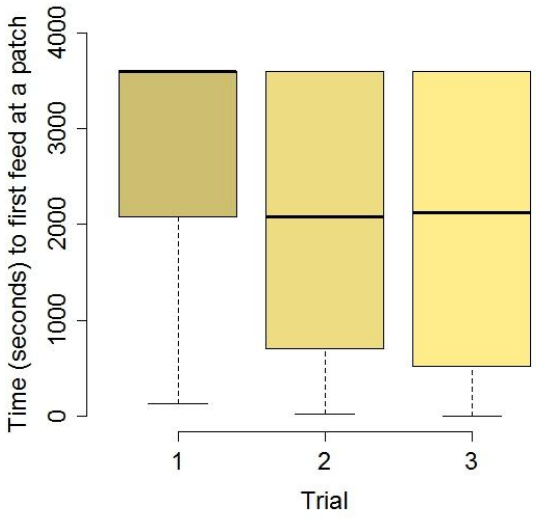


Figure 5.5: Birds' time to first feed at a foraging patch in trials 1, 2, and 3. For graphical representation, birds that failed to feed at either patch are here assigned a ceiling value 'feed time' of 3600 seconds. (Bars denote the median time to first forage; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

Proportion of Group to Feed at a Patch (All Groups)

A *GLMM* revealed no significant interaction between demonstrator condition (present / not present), and trial in the proportion of group members that fed at a patch (Wald test: $z = 0.005$, $p = 0.99$, 95% CI odds ratio = [0.55, 1.82]) Re-running the model with the interaction term removed, there was little evidence for a main effect of demonstrator condition (Wald test: $z = -0.48$, $p = 0.63$), with the odds of birds feeding at a patch being 0.88x as great (95% CI = [0.53, 1.46]) when demonstrators were present than when they were absent (Fig. 5.6). The odds of birds feeding at a patch, however, were estimated at 1.98x (95% CI = [1.47, 2.67]) higher in trial 3 than in trial 1 (Wald test: $z = 2.25$, $p = 0.024$) (Fig. 5.7).

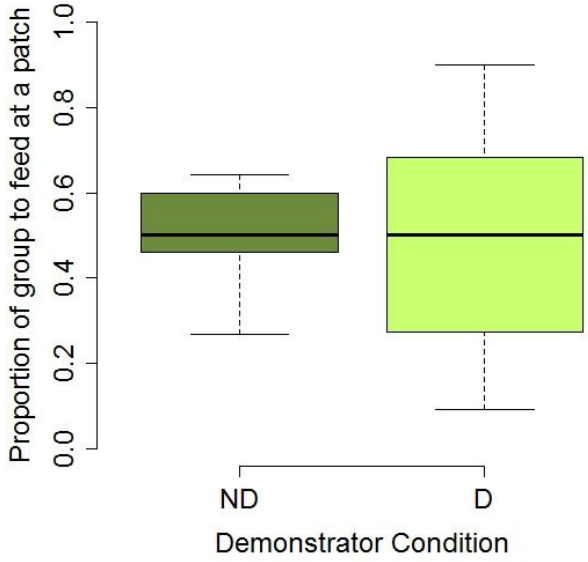


Figure 5.6: Proportion of group to feed at a foraging patch in a given trial under no demonstrator present (ND) versus demonstrator present (D) conditions. (Bars denote the median proportion of group members that fed; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

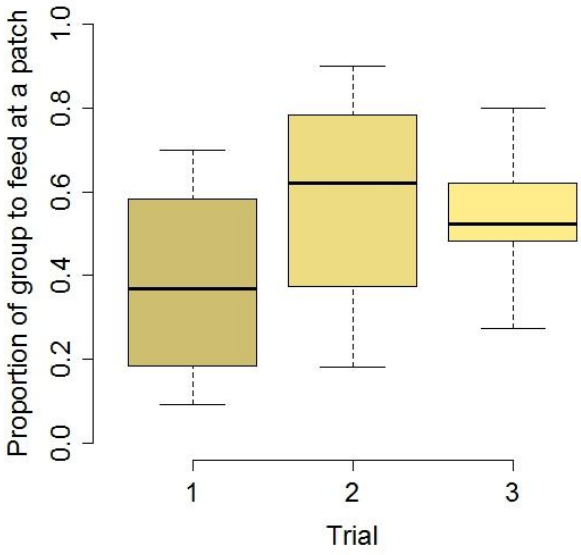


Figure 5.7: Proportion of group to feed at a foraging patch in trials 1, 2, and 3. (Bars denote the median proportion of group members that fed; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

Proportion of Group to Feed First at the Demonstrated Patch versus the Non-demonstrated Patch (Demonstrator-containing Groups Only)

A *GLMM* revealed no significant interaction between the proportion of group members that fed first at the patch the demonstrators in their group had been trained to feed at (the demonstrated patch) relative to the proportion of group members that fed first at the opposite patch (the non-demonstrated patch), and trial (Wald test: z = -0.49, p = 0.62, 95% CI odds ratio = [0.44, 1.64]) (though the ratio of the proportion of birds feeding first at the demonstrated patch compared to the non-demonstrated patch did appear to decrease slightly over time, being 0.72x as great in trial 3 as in trial 1 (95% CI = [0.37, 1.39])).

Re-running the model with the interaction term removed, there was strong evidence for a main effect of demonstrated patch (Wald test: z = 3.25, p = 0.0012), with the odds of birds feeding first at the demonstrated patch being 2.44x higher (95% CI = [1.42, 4.17]) than the odds of birds feeding first at the non-demonstrated patch (Fig. 5.8). The odds of birds feeding at either one of the available patches (demonstrated or non-demonstrated) were estimated at 1.61x greater in trial 3 than in trial 1 (95% CI = [1.17, 2.23]), although this effect did not reach significance (Wald test: z = 1.46, p = 0.15) (Fig. 5.9).

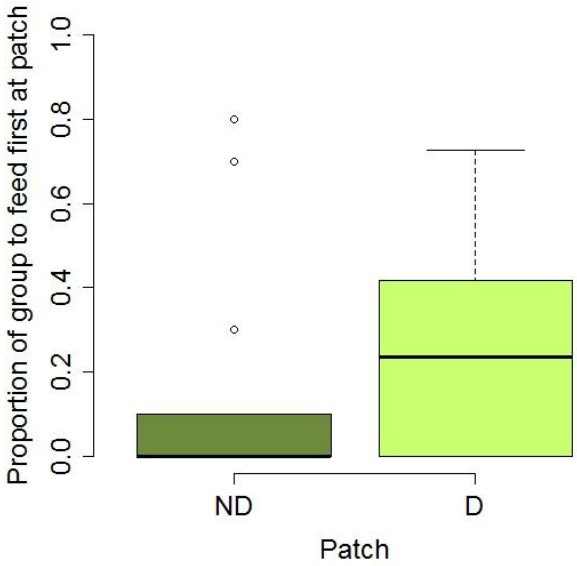


Figure 5.8: Proportion of group to feed first at non-demonstrated (ND) versus demonstrated (D) foraging patch in a given trial (note that some group members did not feed at either patch). (Bars denote the median proportion of foragers at a patch; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

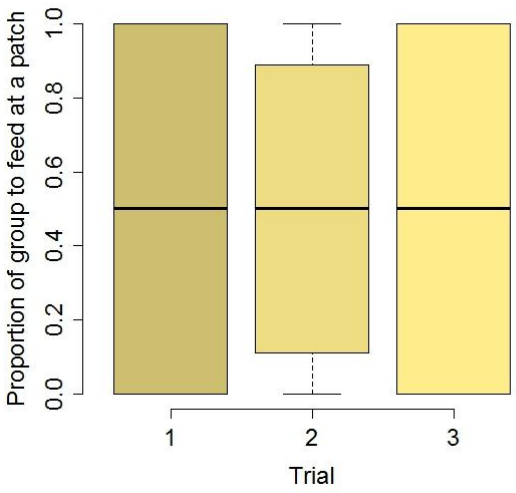


Figure 5.9: Proportion of group to feed at a foraging patch in trials 1, 2, and 3. (Bars denote the median proportion of foragers at a patch; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

Condition 2

Time to First Feed at Familiar Patch (All Groups)

In a Cox Proportional Hazards Model containing data from all group members, there was no significant interaction between groups' prior knowledge state (uniform / split) and trial in the time birds took to first feed at the patch with which they were familiar (Wald test: χ^2 = 0.42, df =1, p = 0.52, 95% CI = [0.56, 1.34]). Upon removing the interaction term, there was no evidence of a significant difference according to groups' prior knowledge states (Wald test: χ^2 = 0.18, df =1, p = 0.67), with birds in split groups typically feeding for the first time at the patch with which they were already familiar 0.92x as fast as those in uniform groups (95% CI = [0.62, 1.35]) (Fig. 5.10). There was some evidence (though this did not reach significance) of a difference in birds' first feeding times at familiar patches across trials (Wald test: χ^2 =

2.00, df =1, p = 0.16), with birds typically feeding for the first time at the familiar patch 1.37x faster in trial 3 than in trial 1 (95% CI = [1.10, 1.37]) (Fig. 5.11).

When the model was re-run excluding the two birds in each group that were familiar with patch '*b*' (the minority group in the split prior knowledge condition), there was again no significant interaction between groups' prior knowledge state (uniform / split) and trial in the time birds took to first feed at the patch with which they were familiar (Wald test: χ^2 = 0.51, df =1, p = 0.48, 95% CI = [0.53, 1.35]). Upon removing the interaction term, there was no strong evidence of a significant difference according to groups' prior knowledge states (Wald test: χ^2 = 1.62, df =1, p = 0.20), with birds in split groups typically feeding for the first time at the patch with which they were already familiar 0.76x as fast as those in uniform groups (95% CI = [0.50, 1.16]) (Fig. 5.10). There was also no strong evidence of a difference in birds' first feeding times at familiar patches across trials (Wald test: χ^2 = 1.81, df =1, p = 0.18), with birds typically feeding for the first time at the familiar patch 1.38x faster in trial 3 than in trial 1 (95% CI = [1.09, 1.74]) (Fig. 5.11).

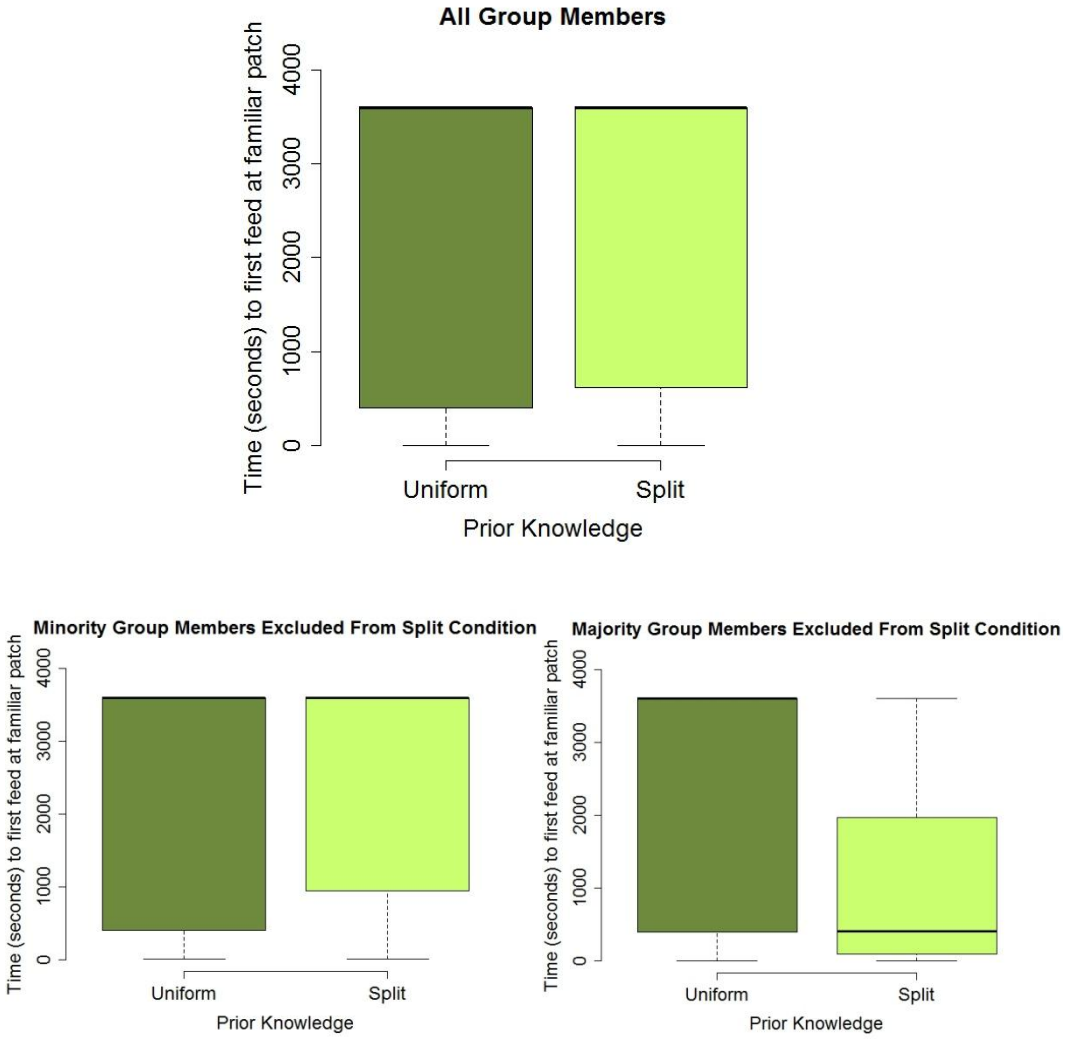


Figure 5.10: Birds' time to first feed at a familiar foraging patch in a given trial under uniform and split prior knowledge conditions. For graphical representation, birds that failed to feed at the patch are here assigned a ceiling value 'feed time' of 3600 seconds. (Bars denote the median time to first forage; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

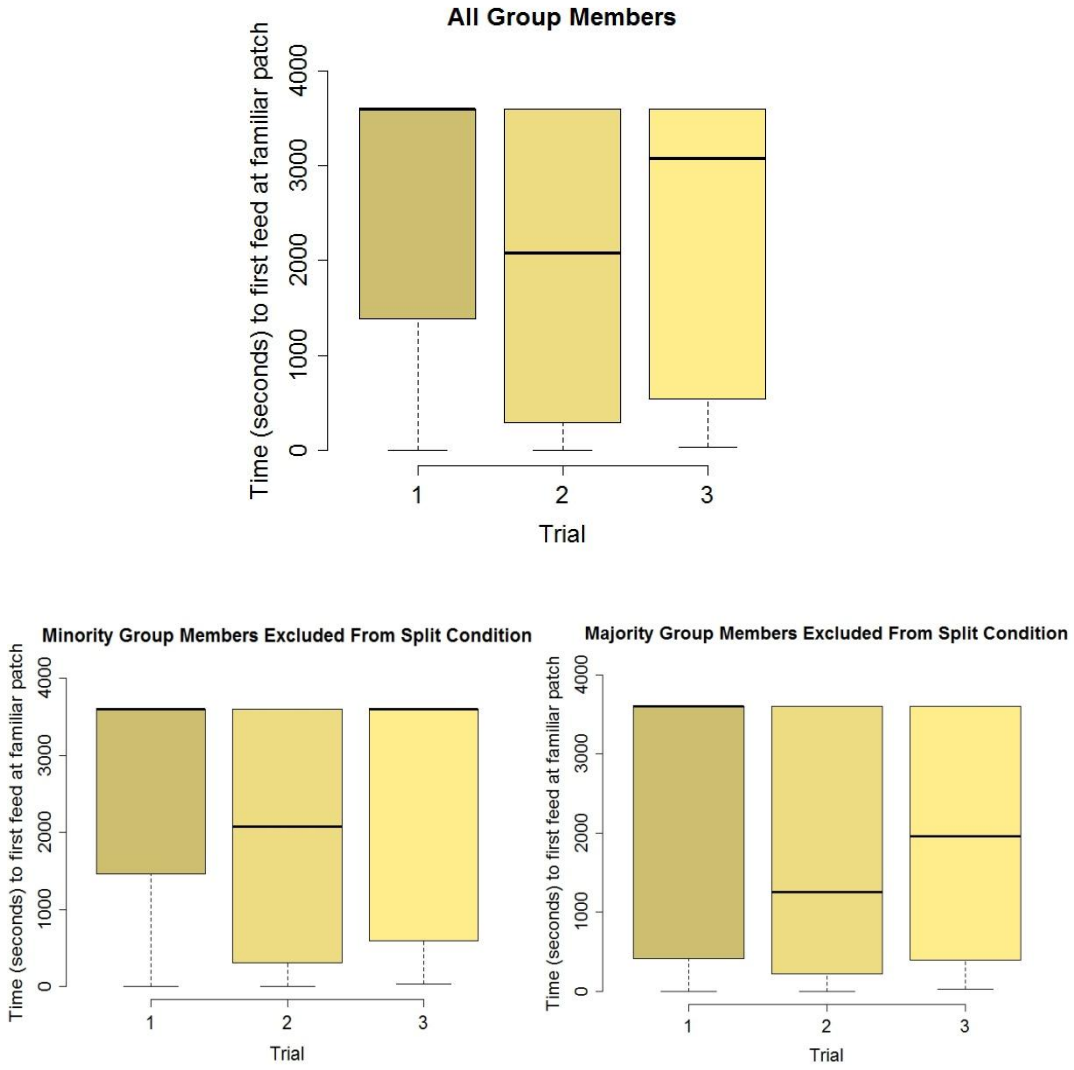


Figure 5.11: Birds' time to first feed at a familiar foraging patch in trials 1, 2, and 3. For graphical representation, birds that failed to feed at the patch are here assigned a ceiling value 'feed time' of 3600 seconds. (Bars denote the median time to first forage; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

Time to First Feed at Unfamiliar Patch (All Groups)

In a Cox Proportional Hazards Model containing data from all group members, there was a significant interaction between groups' prior knowledge state (uniform / split) and trial in the time birds took to first feed at the patch with which they were

unfamiliar (Wald test: χ^2 = 4.07, df =1, p = 0.044). When groups' prior knowledge was split, birds fed at the patch that was unfamiliar to them 0.67x as fast in trial 3 as in trial 1 (95% CI = [0.48, 0.93]). When groups' prior knowledge was uniform, however, birds fed at the patch that was unfamiliar to them 1.83x faster in trial 3 than in trial 1 (95% CI = [1.27, 2.65]). The ratio of the time taken by birds to approach the unfamiliar patch when groups' prior knowledge was split, as opposed to when it was uniform, was estimated as 0.37x (95% CI = [0.22, 0.60]) as great in trial 3 as in trial 1 (Fig. 5.12).

When the model was re-run excluding the two birds in each group that were familiar with patch '*b*' (the minority group in the split prior knowledge condition), there remained some evidence of an interaction between groups' prior knowledge state (uniform / split) and trial in the time birds took to first feed at the patch with which they were unfamiliar, though this did not reach significance (Wald test: χ^2 = 2.30, df =1, p = 0.13). When groups' prior knowledge was split, birds fed at the patch that was unfamiliar to them 0.85x as fast in trial 3 as in trial 1 (95% CI = [0.52, 1.19]). When groups' prior knowledge was uniform, however, birds fed at the patch that was unfamiliar to them 1.85x faster in trial 3 than in trial 1 (95% CI = [0.61, 1.20]). The ratio of the time taken by birds to approach the unfamiliar patch when groups' prior knowledge was split, as opposed to when it was uniform, was estimated as 0.46x (95% CI = [0.28, 0.76]) as great in trial 3 as in trial 1 (Fig. 5.12).

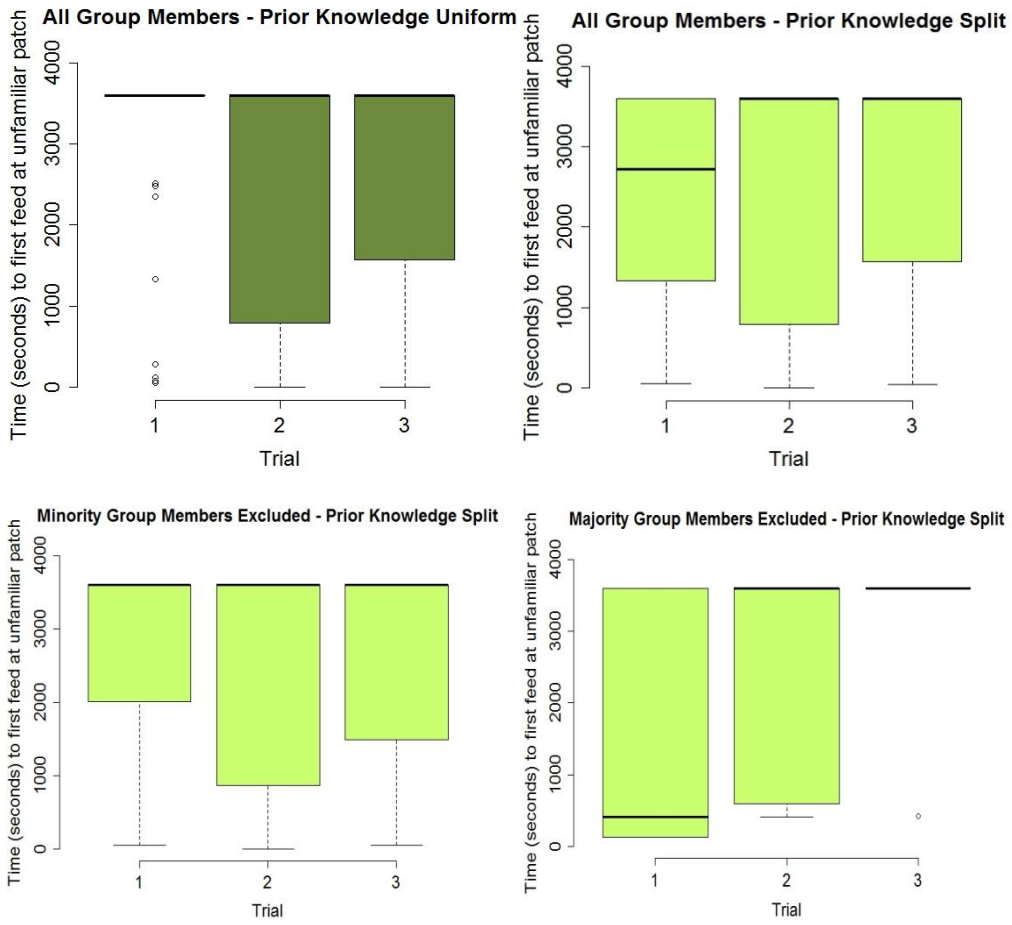


Figure 5.12: Birds' time to first feed at an unfamiliar foraging patch over the course of trials 1-3 under uniform and split prior knowledge conditions. For graphical representation, birds that failed to feed at the patch at all are here assigned a ceiling value 'feed time' of 3600 seconds. (Bars denote the median time to first forage; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

Proportion of Group to Feed at Familiar Patch First (All Groups)

In a *GLMM* containing data from all group members, differences in the proportion of birds that fed first at the patch they had been pre-exposed to (were familiar with), depending on whether or not their group's prior knowledge state was uniform or split, did not alter significantly across trials (Wald test: z = -0.34, p = 0.73, 95% CI odds ratio = [0.48, 1.68]). After this non-significant interaction term was removed, there

was no evidence for a main effect of groups' prior knowledge state (uniform or split) on birds' tendency to visit the patch with which they were familiar before visiting the patch with which they were unfamiliar (Wald test: $z = 0.089$, $p = 0.93$), with the odds of birds visiting the familiar patch first being 0.98x as great when a group's prior knowledge state was uniform than when it was split (95% CI = [0.58, 1.64]) (Fig.5.13). The odds of birds feeding at the familiar patch before the unfamiliar patch were estimated at 1.66x greater in trial 3 than in trial 1, but this effect did not reach significance (Wald test: z = 1.59, $p = 0.11$, 95% CI = [1.22, 2.28]) (Fig. 5.14).

When the model was re-run excluding the two birds in each group that were familiar with patch '*b*' (the minority group in the split prior knowledge condition), differences in the proportion of birds that fed first at the patch they had been pre-exposed to (were familiar with), depending on whether or not their group's prior knowledge state was uniform or split, again, did not alter significantly across trials (Wald test: $z = -0.55$, $p = 0.58$, 95% CI odds ratio = [0.43, 1.60]). After this non-significant interaction term was removed, there was little evidence for a main effect of groups' prior knowledge state (uniform or split) on birds' tendency to visit the patch with which they were familiar before visiting the patch with which they were unfamiliar (Wald test: $z = -0.27$, $p = 0.79$), with the odds of birds visiting the familiar patch first being 1.08x greater when a group's prior knowledge state was uniform rather than split (95% CI = [0.63, 1.86]) (Fig.5.13). The odds of birds feeding at the familiar patch before the unfamiliar patch were estimated at 1.57x greater in trial 3 than in trial 1, but this effect did not reach significance (Wald test: z = 1.36, $p = 0.18$, 95% CI = [1.13, 2.18]) (Fig. 5.14).

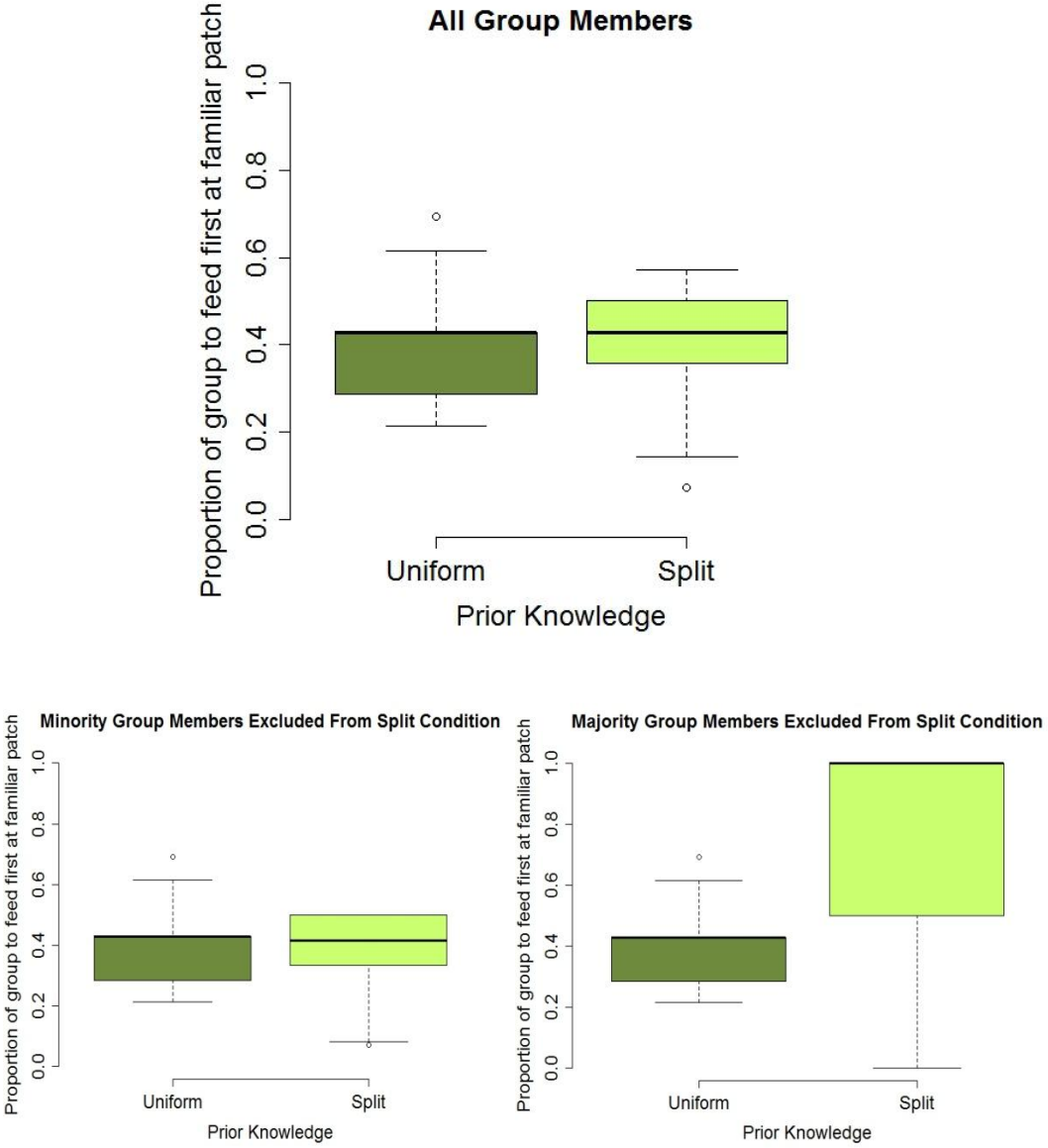


Figure 5.13: Proportion of group to feed first at familiar foraging patch under uniform and split prior knowledge conditions. (Bars denote the median time to first forage; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

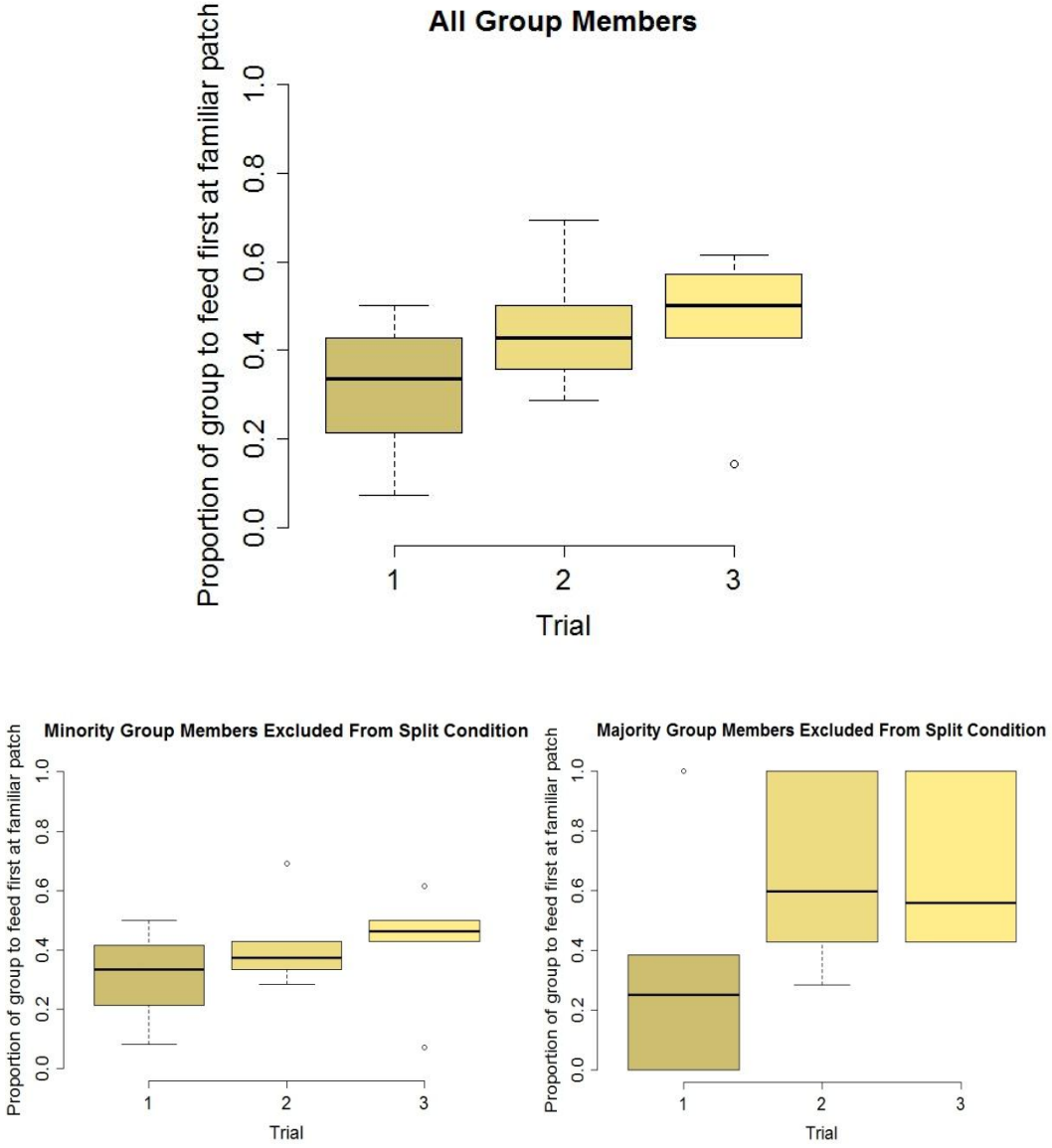


Figure 5.14: Proportion of group to feed first at familiar foraging patch in trials 1, 2, and 3. (Bars denote the median time to first forage; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

Proportion of Group to Feed at Unfamiliar Patch First (All Groups)

In a *GLMM* containing data from all group members, differences in the proportion of birds that fed first at the patch they had not been pre-exposed to (were unfamiliar with), depending on whether or not their group's prior knowledge state was uniform or split, did not alter significantly across trials (Wald test: $z = -0.69$, $p = 0.49$, 95% CI

odds ratio = [0.38, 1.59]). After this non-significant interaction term was removed, there was evidence for a main effect of groups' prior knowledge state (uniform or split) on birds' tendency to visit the patch with which they were unfamiliar before visiting the patch with which they were familiar (Wald test: z = 3.05, p = 0.0023), with the odds of birds visiting the unfamiliar patch first being 0.33x as great when a group's prior knowledge state was uniform than when it was split (95% CI = [0.16, 0.67]) (Fig.5.15). The odds of birds feeding at the unfamiliar patch before the familiar patch were estimated at 0.98x as great in trial 3 than in trial 1. This effect was not significant (Wald test: z = -0.039, p = 0.97, 95% CI = [0.69, 1.40]) (Fig. 5.16).

When the model was re-run excluding the two birds in each group that were familiar with patch '*b*' (the minority group in the split prior knowledge condition), differences in the proportion of birds that fed first at the patch they had not been pre-exposed to (were unfamiliar with), depending on whether or not their group's prior knowledge state was uniform or split, again, did not alter significantly across trials (Wald test: z = -0.31, p = 0.76, 95% CI odds ratio = [0.42, 1.87]). After this non-significant interaction term was removed, there was evidence for a main effect of groups' prior knowledge state (uniform or split) on birds' tendency to visit the patch with which they were unfamiliar before visiting the patch with which they were familiar (Wald test: z = 2.82, p = 0.0047), with the odds of birds visiting the unfamiliar patch first being 0.38x as great when a group's prior knowledge state was uniform than when it was split (95% CI = [0.19, 0.74]) (Fig.5.15). The odds of birds feeding at the unfamiliar patch before the familiar patch were estimated at 1.21x greater in trial 3 than in trial 1, but this effect did not reach significance (Wald test: z = 0.50, p = 0.62, 95% CI = [0.83, 1.75]) (Fig. 5.16).

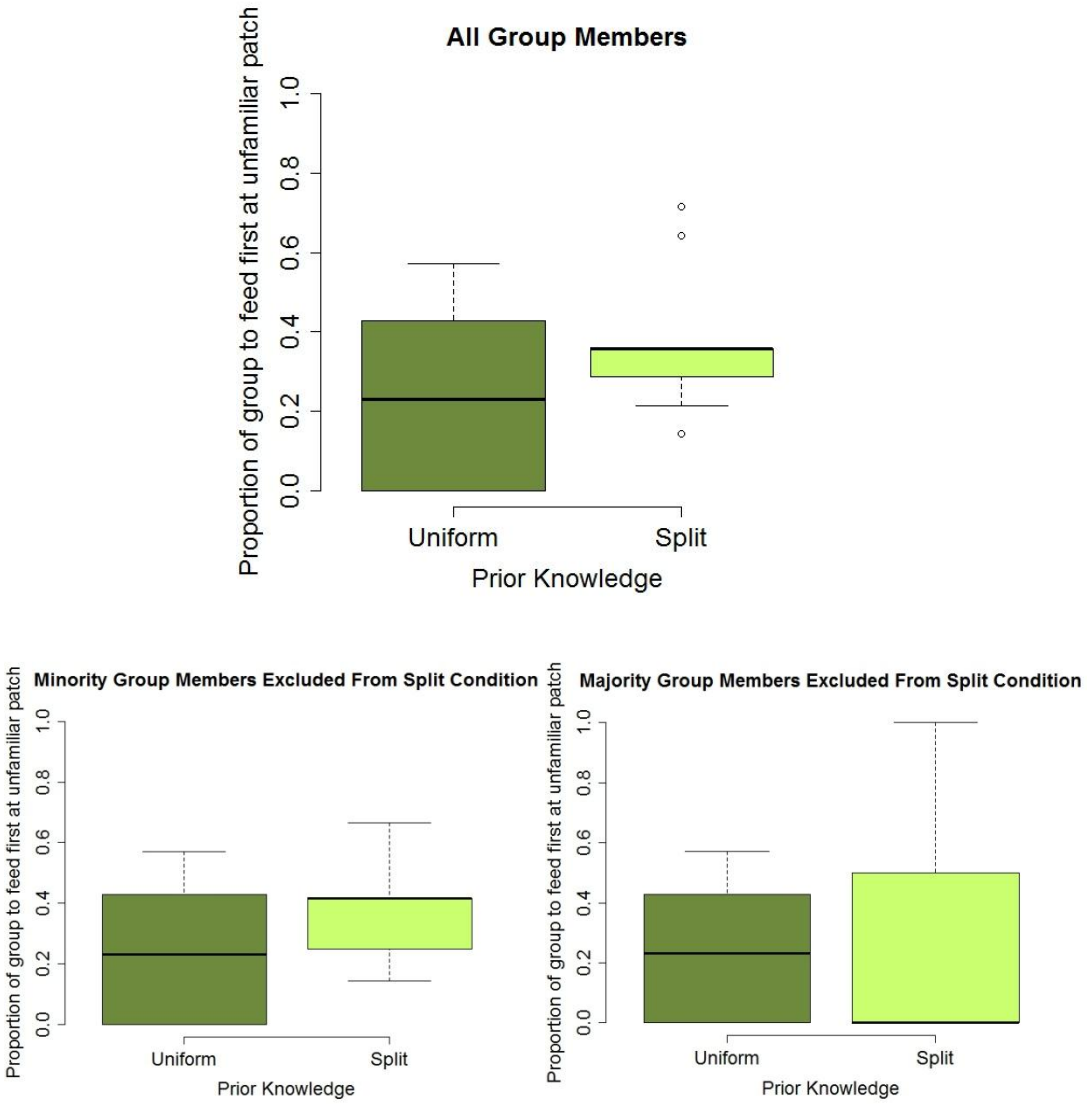


Figure 5.15: Proportion of group to feed first at unfamiliar foraging patch under uniform and split prior knowledge conditions. (Bars denote the median time to first forage; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

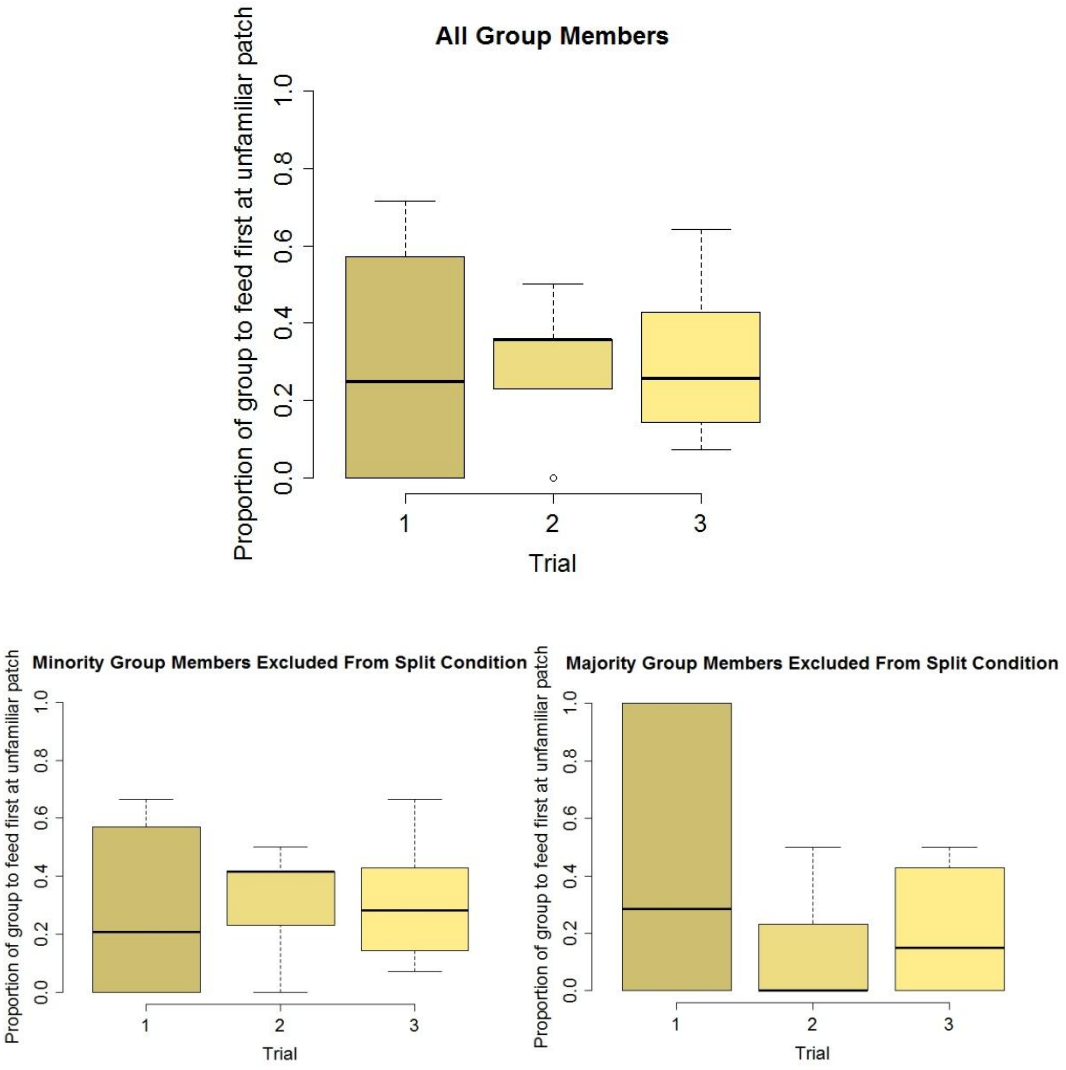


Figure 5.16: Proportion of group to feed first at unfamiliar foraging patch in trials 1, 2, and 3. (Bars denote the median time to first forage; boxes denote the inter-quartile range; and whiskers denote 1.5x the inter-quartile range.)

Discussion

In this study, I presented three groups (Condition1) / two groups (Condition 2) of budgerigars with a series of pairs of novel foraging patches. Each member of a pair was visually distinct, and positioned at opposite ends of a group's enclosure. In the first set of tests (Condition 1), all or most group members had no prior information

relating to either foraging patch. In some cases, however, two birds in the group (demonstrators) were given prior exposure to one member of a given pair. In the second set of tests (Condition 2), group members had prior personal information relating to one member of each patch pair. In some cases, all group members had prior information about the same member of a given pair of patches, whereas in others, two members of the group were given prior exposure to the opposite member of a pair of patches than were the rest of their group.

Predictions 1 and 2

In Condition 1, I found no difference in the time taken by naïve birds to feed from a patch for the first time, or in the proportion of naïve birds that fed at a patch in a given trial, depending on whether or not their group contained demonstrators with prior knowledge that one of the two patches contained food (Fig. 5.4, 5.6). This was inconsistent with my first prediction. I had expected birds in groups containing demonstrators to exhibit a greater propensity to feed at patches than birds in groups containing no demonstrators. This was because I anticipated that demonstrators would no longer be neophobic towards the member of a patch pair with which they had prior experience, whereas birds with no experience of either member of a patch pair would be neophobic towards both. Thus, I expected demonstrators to be less hesitant to feed (at the patch they were already familiar with) at the start of trials, than birds with no experience of either patch. Assuming the social information provided by foraging demonstrators would attract naïve birds to a patch (my second prediction), I therefore expected naïve birds in groups seeded with demonstrators to be more likely, and quicker, to feed at a patch for the first time than those in unseeded groups.

In reality, although demonstrators were typically the first birds in their group to feed at a patch, and usually fed from patches at least as quickly during trials as they did during pre-training, they were often no quicker to feed than were one or two 'pioneer' birds in those groups initially composed entirely of naïve birds – with the result that feeding bouts at patches were often initiated at approximately the same time in both demonstrator present and demonstrator not present trials. A possible explanation for this is that all birds were food deprived for one hour before trials commenced. Coupled with the fact that millet seeds are a highly desirable food for budgerigars, and that food was easily visible and readily accessible from the patches presented, this is likely to have meant that group members were motivated to forage at patches from an early stage. In some individuals, this motivation may have been sufficient to enable them to overcome any unwillingness to investigate a potentially dangerous new object (especially since all the birds used in this study had been exposed to novel foraging objects repeatedly over the course of previous experiments, which may have meant that they did not view the variants presented to them during this set of experiments as being entirely 'new' objects), almost as quickly as demonstrators fed at the patch they were already familiar with. It is also possible that social information generated by one or two pioneers that were quick to visit patches in groups that did not contain demonstrators, may have been of a similar strength to that generated by the two pre-trained demonstrators present in other groups. Had groups contained a greater number of demonstrators, it is possible that these might have been able to provide stronger, more salient, social information to the naïve birds in their group. In turn, this might have meant that, even if pioneers and demonstrators themselves happened to arrive at patches at approximately the same time, foraging behaviour amongst remaining naïve group members would nonetheless have subsequently spread more rapidly under

conditions in which demonstrators were present than it did under conditions in which they were not present (assuming, of course, that birds were not deterred from visiting patches at which there were a large number of potential competitors). (For a possible explanation of why some birds, irrespective of whether or not their groups contained demonstrators, failed to feed at patches at all, see also Discussion, Chapter Six.)

In accordance with my second prediction, however, I *did* find that when a group contained demonstrators, more naïve birds tended to feed first from the demonstrated foraging patch than fed first from the non-demonstrated patch (Fig. 5.8, 5.9). Consistent with existing empirical work (e.g., Templeton and Giraldeau, 1996; Rafacz and Templeton, 2003), this suggests that, in the absence of any prior personal information, budgerigars may adopt a 'copy / feed in the same location as others when uncertain' strategy (Laland, 2004) and use the social information provided by others to inform their foraging choices. In the case of this particular experiment, it is possible that birds' preference for the foraging patch they had seen demonstrators feeding at, may have arisen primarily as a result of a tendency to flock together. Theoretical work by Boyd and Richerson (1985, 1988) and Laland *et al.* (1996) proposed that individuals lacking in personal information may be especially likely to rely on social information to guide their decision making if personal information is 'costly' to acquire. This has been found to be the case in guppies, which have been shown to adopt the same route to food sources taken by knowledgeable demonstrators, even when other more direct routes are available (Laland and Williams, 1997, 1998) – presumably because the protection gained through aggregating with other individuals generally outweighs the alternative gain of more rapid, unimpeded access to a food source that might be made possible by individual exploration and greater reliance on

personal information. Thus, naïve budgerigars in this study may have favoured the foraging patch selected by their group's demonstrators, over the alternative, non-demonstrated patch, because they were initially uncertain as to the location of profitable foraging locations, and/or because they preferred to forage in the proximity of other birds rather than on their own.

Favouring social information over individual exploration when faced with decisions about where to forage, and what to forage on, may confer a number of benefits. In their native Australia, budgerigars are subject to predation by snakes as well as other birds (Wyndham, 1980; Radtke, 1988), and joining other members of their flock already at a particular site, rather than continuing to search independently for another foraging site, may reduce individuals' risk of being predated (Krebs and Davies, 1993). Following others to a food source – at least in the wild, where seed clusters may presumably often be widely dispersed – may also help naïve individuals find and access food more quickly than they would if they were to ignore available social information and obtain food by means of individual exploration alone.

Predictions 3, 4 and 5

In Condition 2, my results produced some support for my third prediction, which was that birds would tend to feed at the patch they had prior personal information about (and thus knew was a profitable food source), before they fed at the patch they lacked personal information about. When all group members had prior information about the same member of a particular pair of patches (uniform prior knowledge), approximately 40% of group members fed first at the patch with which they were

already familiar, whereas only 20% fed first at the patch they had not encountered during pre-training (the remaining 40% did not feed at either patch). When most group members had prior information about the same patch, but two group members had prior information about the opposite patch (split prior knowledge), approximately 45% of individuals fed at the patch they were already familiar with, whilst 35% fed first at the patch they had not encountered during training (the remaining 20% did not feed at either patch) (Fig. 5.13, 5.15). This also provided some support for my fourth prediction, which was that birds' preferences for the familiar patch would be less marked when groups contained two birds possessing prior personal information that conflicted with that of the rest of the group, than when they did not.

Contrary to expectations, however, I found little evidence to support my fifth prediction, which was that in the split condition, any preference for the unfamiliar patch would be relatively more marked in the minority group than in the majority group (i.e., that a motivation to maintain close to the rest of their group might override these birds' preference for personal over social information). Approximately 45% of birds in the majority groups fed first at the patch with which they were already familiar, compared to approximately 40% who fed first at the patch they had not encountered during pre-training; whereas approximately 65% of birds in the minority groups fed first at the patch with which they were already familiar, compared to approximately 30% who fed first at the patch they had not encountered during pre-training (Fig. 5.13, 5.15). Moreover, re-running my analyses with birds from minority groups excluded yielded similar results to those generated in the initial analyses containing all group members. This indicated that birds' relatively greater inclination to feed first at the foraging patch with which they were unfamiliar when in groups

containing split prior knowledge, as opposed to uniform prior knowledge, was not purely attributable to birds in minority groups discounting their prior personal information and joining the rest of their flock mates at the opposite patch.

The first result is consistent with birds weighting prior personal information (and/or current social, non-conflicting information) above no information, and preferring to visit patches that had previously proved both non-dangerous, as well as profitable, to as-yet untested patches. The second result is consistent with some birds weighting prior personal information (and/or current social, non-conflicting information) about the patch to which they had been habituated during pre-training, over any current (conflicting) social information available about the newer patch; and with others weighting new (conflicting) social information about the newer patch, over their existing personal information (and/or current social, non-conflicting information). The third result suggests that birds' weighting of personal and social information may not simply be accounted for by a predisposition to flock together. Indeed, since birds in the minority group of the split prior knowledge condition appeared, if anything, more inclined to first visit the patch with which they were familiar, than did those in the majority group, it may be the case that birds' decisions to use personal versus social information were informed at least partially by a motivation to avoid competition for access to food.

A previous assessment of budgerigars' reliance on social information when foraging (Valone and Giraldeau, 1993) found little evidence that they made use of it – instead, they appeared to rely predominantly on personal patch-sample information and personal prior knowledge of food distribution to assess the quality of a currently

exploited patch. However, whereas Valone and Giraldeau's (1993) study examined budgerigars' patch *departure* choices, this study examined their patch *arrival* choices. As such, when deciding which patch to visit first, birds did not have access to up-to-date patch-sample information, only past personal information and any social information provided by group mates already foraging from one or other of the patches. Thus, it may be the case that budgerigars only ignore current social information when they also have access to current personal (patch-sample) information. If, as in this study, they only have access to (presumably once accurate, but potentially out-dated) personal prior information, their inclination to utilise (possibly less accurate, but up-to-date) current social information may increase. It is also possible that other differences between Valone and Giraldeau's (1993) study and mine, may have contributed to our different findings. For instance, the former assessed the behaviour of budgerigars when foraging in pairs, whereas mine assessed the behaviour of budgerigars housed in groups of 12-14 birds. Potentially, the arrival of several birds at a foraging patch (or conversely, the departure of several birds from a foraging patch) might provide more salient, or persuasive, social information than the arrival at / departure from a foraging patch of just one other bird. In the case of my study, the company of a larger number of birds might also have required budgerigars to make foraging choices aimed at minimising their exposure to competition – causing them perhaps to avoid certain foraging patches (even those about which they possessed prior knowledge) if these were already crowded, and instead seek out new patches about which some social information was available, but at which smaller numbers of birds were gathered.

Indeed, even when all group members had prior information about the same member of a particular pair of patches, not all of them fed at this patch before the one they were unfamiliar with (approximately 20% of birds typically visited the novel patch first). One reason for this could be that competition for access to the familiar patch drove some group members to seek food elsewhere. In addition, while the members of each pair of patches were visually distinguishable, they were nonetheless of comparable size, shape, and overall appearance, as well as being positioned in equally accessible and visible areas of a group's cage. The purpose of this was to minimise any intrinsic differences in the attractiveness of one member in a pair relative to the other. However, a side-effect of this could have been that birds with prior experience of one patch were able rapidly to generalise, to some extent, to the other patch, and may not have regarded it as being entirely novel. This may have made some birds willing to feed at it, even in the absence of any social information being provided about it by other members of their group.

Predictions 6 and 7

In demonstrator-containing groups in Condition 1, I found relatively little change (slight decreases) in the proportion of naïve birds that visited the demonstrated versus the non-demonstrated patch first over the course of trials 1-3. In Condition 2, I also found little change in the proportion of birds that fed first at the patch they were already familiar with across trials 1-3 (Fig. 5.14), or in the proportion of birds that fed first at the patch they were initially unfamiliar with across trials 1-3 (Fig. 5.16). I therefore did not find strong support for my sixth prediction, which was that individuals' initial patch preferences would become less marked across repeated

presentations of a given pair of patches. The major reason for this, though – particularly in split prior knowledge groups in Condition 2 – was not because birds maintained a strong preference to feed at one patch before the other across all trials, but rather because they exhibited relatively weak preferences for one patch over the other from trial 1 onwards.

Certainly, groups did not appear to establish 'traditions' and consistently visit one patch in preference to the other (even in Condition 1, where birds exhibited a relatively marked preference to feed first at the same patch as their demonstrators over all three trials, this preference showed signs of decreasing, and may well have eroded further given several more trials). While birds may initially have been slightly more likely to visit patches about which they had prior personal information, or current social information, over patches about which they had no information, they evidently soon began to discover / explore / generalise towards (and thus increase their own personal information, and other group members' social information about) the patch about which they were initially naïve – sometimes even in trial 1.

As in Thornton and Malapert's (2009) meerkat study, the foraging patches presented to birds in this study differed arbitrarily in appearance, but were functionally equivalent (i.e., contained the same amount of food, accessible using the same actions). Furthermore, each member of a pair was positioned only a short distance away from the other during presentations, such that birds could easily see both patches at any one time, and easily move between the two. It is possible that, as seemed to be the case in Thornton and Malapert's meerkats, budgerigars' interactions with one member of a pair of foraging patches may have in fact promoted their

subsequent investigations of the second, very similar alternative patch close by. At the very least, foraging at one patch appeared to have no inhibitory effect on birds' exploration of the alternate patch.

Weighting prior personal, and/or current social information, above individual exploration of an as-yet untested foraging location, may well confer benefits in terms of reduced predation risk and/or reduced time spent searching for food (Laland, 2004). When, however, a food source depletes over time, and/or is monopolisable by a sub-set of individuals within a foraging group (both of which were true here – perching space on patches themselves was usually sufficient for two to three birds at most, and birds already feeding at a patch would often attempt to defend it from newcomers, behaving aggressively towards them and sometimes driving them away), it may become necessary for individuals to search for and investigate alternatives, especially when the costs associated with such activity (such as travel time, or increased vulnerability to predation caused by separation from the rest of the group) are low. This may therefore also explain why any initial preferences budgerigars may have had for patches about which they had prior personal and/or current social information, over those about which they lacked prior personal and/or current social information, were relatively weak from the outset.

In accordance with my seventh prediction, in Condition 1, I found that birds' latencies to feed at a patch for the first time tended to decrease across repeated trials (Fig. 5.5). As birds' exposure to both patches in a pair increased, it is likely that any initial neophobia they had towards them decreased, making them less hesitant to visit and begin interacting with them. As, over time, more birds gained experience of feeding

from the patches, inter-bird competition for access to them also increased. Coupled with increasing familiarity with the patches, this may have encouraged at least some individuals to approach and begin interacting with them from an earlier time in trials 2 and 3 than they did in trial 1. In Condition 2, birds' latency to feed at the patch with which they were already familiar did not decrease significantly across repeated trials (Fig. 5.11) – presumably because in this case they were not neophobic towards the patch in question, and competition for access to the patch was high from the outset of test trials. In uniform prior knowledge patch presentations, birds' latency to feed at the unfamiliar patch, however, did decrease across repeated trials – presumably, as in Condition 1, because birds became less neophobic towards, and increasingly competitive over, this patch over the course of trials 1-3. In contrast, when groups contained split prior knowledge, this effect was largely absent (if anything, birds were marginally slower to approach the unfamiliar patch in trial 3 than they had been in trial 1). Here, birds' prior knowledge of one member in each pair of (essentially similar) patches, coupled with the early provision, by other group members, of social information about the opposite patch, seems to have ensured that they were able to generalise to both patches almost straightaway (Fig. 5.12).

Conclusions

In this study, I investigated budgerigars' reliance on prior personal information, current social information, and individual exploration in deciding when and where to forage. I found that, in the absence of prior personal information, at least some birds appeared to exploit the social information provided by knowledgeable members of their group, feeding at the same patch as them before exploring the other available

patch in their cage. When all the birds in a group possessed prior personal information about one foraging patch but not the other, I found that they tended to visit this patch before the other one. However, when birds had access to social information that conflicted with their prior personal information (i.e., when some birds in a group had prior personal information about one patch, while others had prior personal information about the other), I found evidence for mixed use of personal and social information among individual birds. Over time, budgerigars generally became faster to visit patches, and any initial group-level preferences for one member of a pair of patches over the other were (a) weak from the outset and (b) diminished somewhat over time as birds explored the available alternative. Thus, no enduring foraging traditions appeared to form.

Future Work

A useful extension of this study might include an assessment not only of birds' arrival times at patches, but also of their feeding durations at them, and departure times from them. Such an undertaking would then allow more direct comparisons to be drawn between this and Valone and Giraldeau's (1993) study.

The study would also be improved by the inclusion of data from a greater number of budgerigar groups – particularly the analysis of birds' behaviour under Condition 2, in which only two groups were studied. Ideally, a minimum of four groups would be studied, in order to ensure that each of a given pair of foraging patches could be presented in every possible combination of forms (i.e., in the uniform condition, one group could be pre-trained to feed at patch '*a*', and another to feed at patch '*b*'; whilst

in the spilt condition, one majority group could be pre-trained to feed at patch '*a*' (and the minority group to feed at patch '*b*'), while the other majority group could be pre-trained to feed at patch '*b*' (and the minority group to feed at patch '*a*')). In the two groups used in the current study, birds in the uniform condition were pre-trained to feed from patch '*a*' of a particular pair, and birds in the majority group in the split condition were also pre-trained to feed from patch '*a*', whilst the two birds in the minority group were given prior exposure to patch '*b*'. Should patches '*a*' and '*b*' of a given pair of patches (for example, the Box pair, in which patch '*a*' was green, and patch '*b*' was red), happen to have differed somewhat in their attractiveness to budgerigars, this might have meant that birds had a greater predisposition to visit one in preference to the other, irrespective of any personal or social information they possessed. Thus, if birds in the minority condition appeared to prefer to feed at patch '*a*' over patch '*b*' during trials (and if very few, if any, birds in the uniform condition, or from the majority group in the split condition, preferred to feed at patch '*b*'), it may have appeared that the minority group birds favoured social information over personal information (or at least, exhibited a flocking tendency) – when in reality, patch '*a*' may for some reason simply have been much more attractive to the birds than was patch '*b*'. Only the inclusion of another two experimental groups, in which (in the uniform condition) all the group and (in the split condition) the majority group had been pre-trained to feed at patch '*b*', whilst the minority group were pre-trained to feed at patch '*a*', would make it possible to tease apart the two possible explanations.

Fortunately, the birds in my study did not appear to exhibit strong preferences for one variant of a patch over the other (no groups entirely avoided one patch over the course of three trials; and in the split condition, at least some members of both the majority

or minority sub-groups remained to feed at the patch they had prior personal information about, before switching to feed at the novel patch). Nonetheless, existing conclusions about birds' relative use of social and personal information when foraging would be strengthened by the collection of further, more counterbalanced data.

It could also be profitable to study each individual's relative tendency to (a) conduct pioneer visits to new foraging patches in the absence of any personal or social information about them; (b) visit new patches once social information, potentially conflicting with their own personal information, became available about them; (c) continue to feed at familiar patches, relying on personal information even in the face of conflicting social information; and/or (d) not feed at any patch. This information could then be compared against, for instance, birds' competitive rank within their group, neophobia levels, and/or nutritional state (body condition) to look for potential underlying influences on individuals' foraging decisions.

In addition, an analysis of whether, and to what extent, birds' weighting of personal and social information is influenced by its nature (i.e., whether a patch is a good source of food, or a poor one) and reliability (i.e., whether a patch consistently contains food, or only sporadically), might also prove informative. In this study, both prior personal and current social information were reliable indicators of food – perhaps explaining why birds may not have exhibited strong preferences for one source of information over the other. Were this to change, it is possible that birds' reliance on one source of information relative to the other might adjust accordingly.

It is also possible that birds' receptivity to social information, especially when it conflicts with their personal information, might be affected by the number of birds acting as 'guides' to a particular foraging location. For example, as in nutmeg manikins (Rieucau and Giraldeau, 2009), observing a large number of guides might effectively override an individual budgerigar's weighting of its prior personal information and cause it to rely primarily on social information. Alternatively, absolute number of guides may be less important in influencing budgerigars' foraging choices than is the public information these guides are able to provide about the 'quality' of a particular patch (which may, for instance, be reflected in each guide's seed intake rate, or feeding duration). The latter seems possible in light of the findings from Condition 2 of the current study. Here, a majority of birds had prior information about one patch and a minority of birds had prior information about the other. Despite this, during test trials, some birds in the majority sub-group fed at the foraging patch familiar to the minority, while those in the minority group did not necessarily switch immediately to feeding at the patch familiar to the majority. Hence, it is possible that raw numbers of birds feeding at particular location may not be the only factor to affect arriving flock mates' foraging choices. Further investigation of the influence of different numbers of guides to patches, and of their feeding activity once at them, would be likely to prove illuminating in gaining greater understanding of budgerigars' use of personal versus social information when foraging.

CHAPTER SIX

SOCIAL NETWORKS AND BUDGERIGAR FORAGING DECISIONS

Abstract

Group foragers such as budgerigars may make use of social information in order to locate and exploit new food patches. However, since social interactions rarely occur completely at random, and individuals often differ in the number and strength of associations that they have to other individuals, it is possible that they may be more likely to pay attention to, and learn from, certain members of their group than from others.

Here, I use Network-based Diffusion Analysis (*NBDA*) to investigate the spread of approaching and feeding behaviour at six different novel foraging patches through three groups of 12-14 captive budgerigars.

I find little evidence to suggest that, during the presentation of the foraging patches within each group's cage, the times at which naïve individuals first approached and first fed at them corresponded closely to the times at which other members of their group first approached and first fed at them. It is possible that individual birds differed in their likelihood of discovering and feeding at the patches, and that each individual's visits to patches occurred quite independently of one another, and were not at all influenced by the activities of their group mates (although this seems unlikely in light of earlier findings (Chapter Five)). Alternatively, it is possible that the *NBDAs* run here underestimated birds' use of social information provided by other members of their group. One potential reason for this is that many individuals made several visits to foraging patches during the course of trials, giving those members of the group that had not yet visited the patch a number of opportunities to follow them. However,

NBDAs were only able to take into account each bird's first visit to a patch, which were sometimes separated widely in time.

Introduction

Budgerigars, *Melopsittacus undulatus*, are group foragers whose movements are determined largely by the location of highly ephemeral food and water supplies (Forshaw and Cooper, 1978). In Chapter Five, I found evidence to suggest that they may make use of social information in order to locate and exploit new food patches. In this Chapter, I aim to investigate the influence of budgerigar groups' social networks on the dynamics of this information transmission.

Traditionally, theoretical and empirical studies have tended to assume that all members of a population are equally likely to transmit or receive information (Reader and Laland, 2000). However, assumptions of free mixing and indiscriminate information sharing may often be unrealistic (Lusseau and Newman, 2004; Krause (*et al.*, 2009), since social interactions rarely occur completely at random, and individuals often differ in their number and strength of associations to other individuals (Croft *et al*., 2008).

Coussi-Korbel and Fragaszy (1995) suggested that animals may be more likely to pay attention to, and learn from, certain members of their group over others. Such 'directed social learning' might take the form of 'strategic' copying (for instance, of older, or more successful group members – Laland, 2004). Perhaps more simply,

animals may tend to make use of social information provided by their nearest neighbours (Ballerini *et al*., 2008) or closest affiliates (Bonnie and de Waal, 2006; Schwab *et al*., 2008a). To date, a variety of phenotypic factors have been found to generate non-random animal networks, including size (Hoare *et al*., 2000), hunger level (Krause, 1993), familiarity (Swaney *et al*., 2001) and sex (Reader and Laland, 2000), and it is possible that these, as well as other factors, may produce association patterns that in turn shape the route of information transmission through groups.

Network-based Diffusion Analysis (*NBDA*) (Franz and Nunn, 2009; Hoppitt *et al*., 2010; Hoppitt and Laland, 2011; Hoppitt and Laland, 2013) is a recently developed method of data analysis that enables the detection and quantification of non-random social transmission, as well as other social effects on behaviour. *NBDA* can be used to infer directed social transmission of information if the change over time in individuals' behaviour patterns (as, for instance, occurs during the diffusion of a novel behaviour through a group) follows association patterns in their social network. The method in this case rests on the assumption that the rate of social transmission between a naïve and an informed animal is linearly proportional to the association between them (Hoppitt and Laland, 2011). *NBDA* can also be used to test for a more general social influence on animals' uptake of new behaviour (i.e., one in which information spreads indiscriminately from one individual to another) if all members of a group are assumed to share an equal level of connection to one another.

Thus far, *NBDA* has been applied to a number of wild and captive animal populations including fish, birds, primates and cetaceans (Hoppitt *et al*., 2010; Kendal *et al*., 2010; Aplin *et al*., 2012; Atton *et al*., 2012; Schnoell and Fichtel, 2012; Allen *et al*., 2013),

sometimes providing strong evidence for the social transmission of information through networks. In their study of the discovery of new foraging patches by three sympatric tit species (family Paridae), Aplin *et al.* (2012) found that the first bird to find a patch did so by chance, mediated by individual differences in searching behaviour; but that although some subsequent arrivals appeared still to discover the patch by chance, others appeared to discover it by means of social information received from connected individuals in their social network. Meanwhile, Allen *et al.* (2013) used *NBDA* to provide a strong case for the social transmission of lobtail feeding, a naturally occurring foraging innovation in humpback whales, *Megaptera novaeangliae*.

Here, I used *NBDA* to investigate the extent to which birds' first approach times and first feeding times at a series of novel foraging patches were related to known (previously measured) association patterns in their group's social network. I predicted that:

1) Birds' first approach times and first feeding times would be influenced by the social network of their group, and that individuals that had a high level of association to one another would be more likely to approach, and feed, at a patch in succession and with more similar latencies, than birds that had a low level of association.
2) However, since the birds in this study were housed in relatively confined spaces in which not only their closest associates, but probably all of the rest of their group were visible for most of the time, it was possible that all birds in a group might, in reality, share a high level of connectedness, even if birds spent

more time in close proximity to certain individuals than to others. In this case, I expected to find evidence at least of a general, if not a directed, social influence on birds' first approach times and first feeding times at each patch – i.e., that even if the spread of approaching and/or feeding behaviour at a foraging patch did not correspond well to a group's association network, the timings of individual birds' first approaches to, and first feeds at, the patch, would nonetheless be clustered.

3) Although birds' first approach and first feeding times at novel foraging patches would be subject to social transmission, individual differences, for instance in exploratory behaviour, might also affect their latency to visit patches. Therefore, I predicted that when *NBDAs* also took certain individual-level variables into account, the apparent importance of the social transmission of information in determining birds' first approach and first feeding times at foraging patches would decrease somewhat. In this chapter, I undertook a simple extension of the conventional *NBDA* to include the individual-level variables age and sex, two variables that I previously studied as potential predictors of budgerigars' latency to solve novel foraging tasks (see Chapter Four).

4) Evidence of social transmission (network-based and/or general) would be stronger with respect to birds' first approach times at patches, than with respect to their first feeding times. This was because as many as half or two thirds of a group of birds were able to approach each patch without having to compete strongly for access to perching space, but the number of birds actually able to feed at a patch at any one time was more limited (perching space on patches themselves was usually sufficient for two to three birds at

most). This meant that delays between one bird and the next first beginning to feed at a patch were more likely to occur than were delays between one bird and the next first approaching it.

Methods

Foraging Patch Approach and Feed Times

The experiments described in Chapter Five involved three one-hour-long presentations of six visually distinctive pairs of foraging patches (the Umbrellas, Hangers, Side Feeders, Baskets, Cubes, and Boxes) to groups of 12-14 budgerigars. The first three pairs of patches were presented to three groups of birds, all or most of whom had received no prior exposure to either patch in each pair before trials began (Condition 1). The second three pairs of patches were presented to two of the original three groups of birds, all or most of whom this time *had* been exposed to of one of the patches in a pair prior to the beginning of trials (Condition 2) (see Chapter Five for full details).

In this Chapter, I used data obtained during the first hour-long presentation of each pair of patches under Condition 1, when three groups of birds were faced with three pairs of unfamiliar patches to investigate and feed from. I watched videos using Windows Media Player and recorded the time at which each bird first approached and first fed from each patch in each pair (i.e., six patches in total) for use in *NBDA*. Birds were deemed to have approached a patch when they were seen to both visually inspect

it – this usually involved orientating the head and stretching the neck towards it – and to make a directional movement towards it bringing them within 20 cm of it. Feeding was defined as per Brockway, 1964a ('the head is held close to food and directed at it. The beak need not necessarily be in contact with the food').

Social Network Data

I collected social network data using a network where each connection from bird '*A*' to bird '*B*' is an estimate of the probability that, at any given time, '*A*' will be the closest individual to '*B*'. I chose this as a plausible measure of how likely '*B*' would be to learn the location of new food sources visited by '*A*'.

Each group was sampled a total of ten times over ten consecutive days immediately prior to the beginning of novel foraging patch presentations, five times in the morning and five times in the afternoon.

For each session of data collection, I collected data on all the birds in a group, obtaining five observations of each bird (50 observations per bird over the course of the ten sessions). This was done by cycling through all the birds in the group and recording, at 30 s intervals, which bird was closest to what was the focal bird for that observation. Once all group members had been sampled once, I waited for five minutes before beginning the next cycle of observations – and so on, until all five observations were complete. This method ensured that observations of each bird, as a focal bird, were further apart in time and had lower autocorrelation, than would have been the case if I had observed a continuous sequence on each bird.

Sometimes, it was not possible to distinguish which bird was closest to the focal bird, in which case its two, or in some cases three, nearest neighbours were noted. On other occasions, the focal bird was far from the rest of the group, and recording its nearest neighbour seemed misleading. In such circumstances, I recorded no nearest neighbour if the closest bird was judged to be >30 cm away. Consequently, the network connection from bird '*A*' to bird '*B*' is really an estimate of the probability that, at any given time, '*A*' was both closest to '*B*' and within 30 cm of it.

Once 50 observations had been obtained for each bird, I created association matrices based upon the proportion of times that each bird was observed with each other member of its group as its nearest neighbour.

As well as constructing social networks based on birds' association patterns, I built an additional set of networks in which all members of a group were assumed to be connected equally to one another. This was because, in the housing arrangements provided, all birds – even those that tended not to associate closely with one another – were typically within sight of one another at all times. Thus, it was possible that, under the circumstances of this particular study, an 'equal connections' network might more accurately represent birds' social networks than did an 'association patterns' network.

Analyses

I ran two series of *NBDAs* to assess whether the timing and sequence with which budgerigars in three different groups (a) approached and (b) fed at each of six novel

foraging patches was correlated with patterns of association between individuals in each group. I then ran a second two series of *NBDAs,* identical to the first except that this time all the birds in each group were assumed to share an equal level of connectedness.

As well as running the above four sets of *NBDAs,* in which the timing and sequence of budgerigars' approach and feeding times at foraging patches were assessed separately for each group and foraging patch in turn, I also ran a further four analyses (addressing the same four questions as those in the previous paragraph) in which data from all three groups and all six foraging patches were assessed collectively. The purpose of this was to gain a more general understanding of the strength of any social transmission that took place with regards to budgerigars' approach / feeding times at novel foraging patches.

In all cases, I used the continuous Time of Acquisition Diffusion Analysis (*TADA*) variant of *NBDA* (Hoppitt *et al*., 2010), which is sensitive not only to the order in which individuals acquire a trait, but also to their latency in acquiring it. Each *TADA* compared a model that inferred social transmission if birds' arrival times at patches were clustered in time, and / or corresponded closely to the association patterns in their groups, against a null model that assumed birds' would arrive at patches at a constant rate, not necessarily in an order that corresponded to association patterns in their groups, and that could also include various individual-level variables (e.g., age and sex) as potential predictors of an individual's latency to first approach or feed at a patch.

The time (in seconds) at which each bird first approached / fed at a given patch, and its position within its group's association matrix, were included in every analysis. In the case of those analyses that assessed birds' activity in all three groups and at all six patches collectively, group was included as a random effect and patch type was included as a fixed effect in order to take into account any inherent differences in each group's propensity to investigate new objects, or in the 'attractiveness' of different patches. In the collective analyses, as well as comparing each social transmission model against a 'simple' null model (one that did not contain any individual-level variables), I also compared it against a null model containing the individual-level variables age (in years) and sex. The analyses run separately for each group and task unfortunately did not contain enough data points for models to run properly when null models included individual-level variables, so in these cases only simple null models were used.

'Demonstrators' (pairs of birds with prior knowledge about a particular patch – see Chapter Five for full details), when present in groups, were identified and accounted for in those *NBDAs* relating to birds' approach and feeding times at the particular patches they were familiar with. (Demonstrators were typically the first members of their group to visit the particular patch about which they, but no other birds, had prior knowledge. Nonetheless, identifying them in the analysis ensured that, should a demonstrator happen to approach or feed at a patch after other, previously naïve, members of its group had done so, such an event would not be recognised as social transmission. Essentially, demonstrators were constrained to act as 'transmitters', but not 'receivers' of social information.)

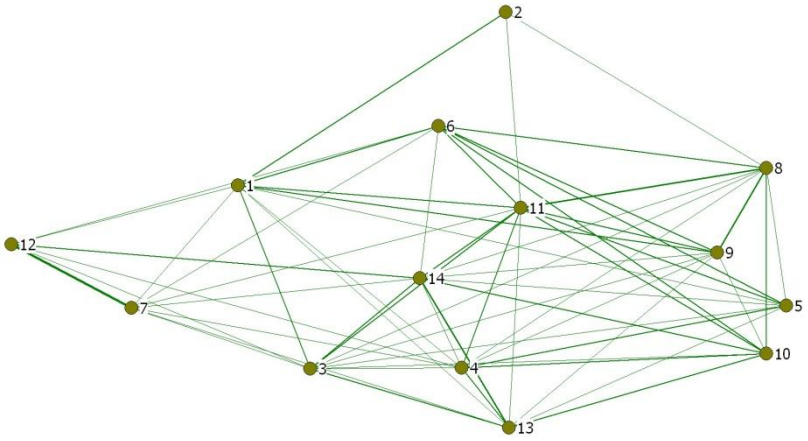
Birds' baseline rates of acquisition (i.e., the rate at which they approached or fed at patches in the absence of social transmission) were assumed to remain constant over time.

Results

Social network data revealed that individual budgerigars often associated closely with one or two other birds in their group, but were connected only weakly to the rest of their group mates. This was particularly marked in Group 2 and Group 3 (Fig. 6.1).

In Group 2, for example, Bird 3 was seen closest to Bird 4 on 50% of sampling occasions, and closest to Bird 11 on 35% of sampling occasions. During the remaining 15% of sampling occasions, its closest associates were Birds 1, 5, 6, 7 and 12. It was never seen in close proximity to Birds 2, 8, 9, 10, or 13.

(*i*)



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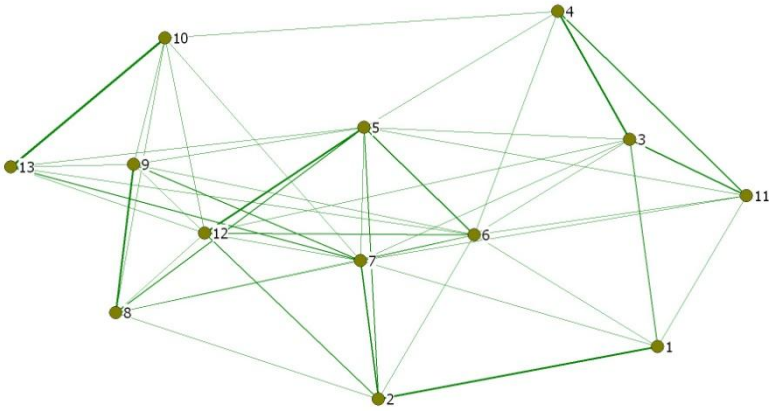

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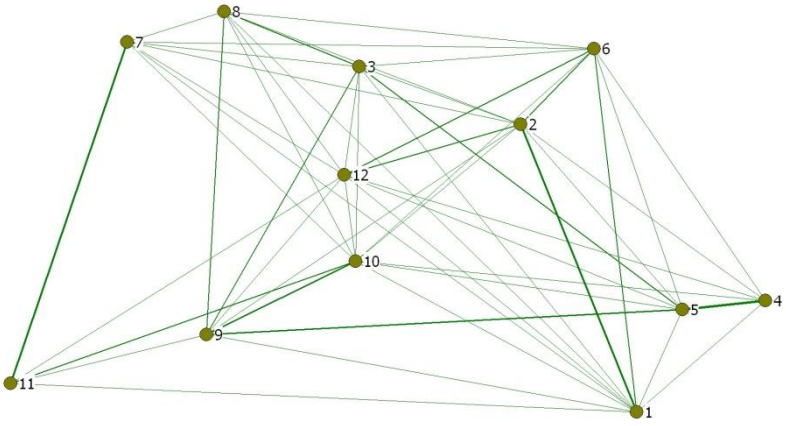


Figure 6.1: Social networks of (i) Group 1, (ii) Group 2 and (iii) Group 3. Line weights indicate association strength. Network layout produced by spring embedding based on geodesic distance.

Not all birds that approached a given foraging patch ultimately fed at it (i.e., the proportion of each group that approached a patch was generally higher than the proportion of the group that subsequently fed at it).

The spread of approaching and/or feeding behaviour through a particular group at a particular patch appeared sometimes to occur between closely associated individuals. In Group 3, for example, after Bird 1 approached 'Side Feeder *a*' for the first time, the next bird to approach it was its closest associate (the bird it had been seen in closest proximity to on 50% of sampling occasions during the collection of group social network data), Bird 2. Once Bird 2 had approached the feeder, the next bird to approach it was Bird 12 – another close associate of Bird 2, having been seen in close proximity to it on 15% of sampling occasions during the collection of group social network data. On other occasions, however, it appeared that this spread of behaviour did not accord closely with the strength of associations between individual birds. In Group 1, for instance, the first bird to feed at 'Hanger *a*' was Bird 6. This was followed by Bird 2, a bird it had never been seen in close proximity to during the collection of social network data. The next bird to approach the patch was Bird 11, which had been seen in close proximity to Bird 2 on only 4% of sampling occasions during the collection of social network data. Bird 11 was followed by Bird 12, which had never been seen in close proximity to Bird 11; next came Bird 13, which had never been seen in close proximity to Bird 12 (Fig. 6.2, 6.3).

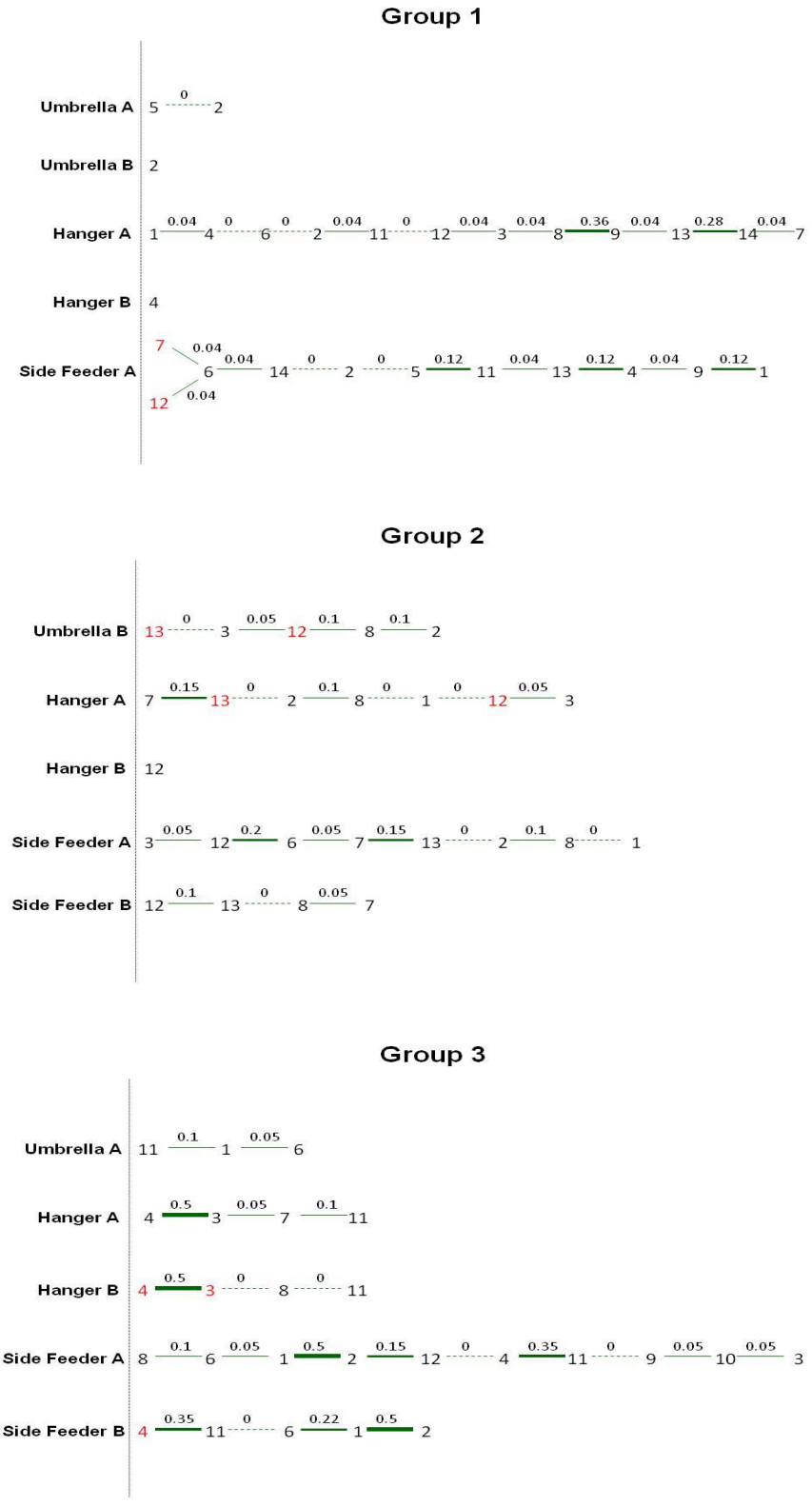


Figure 6.2: Group members' order of approach at each novel foraging patch (from left to right, first to last bird to approach). Association strength (proportion of time spent in close proximity) between one bird and the next indicated by line weight and text above line. Demonstrators depicted in red.

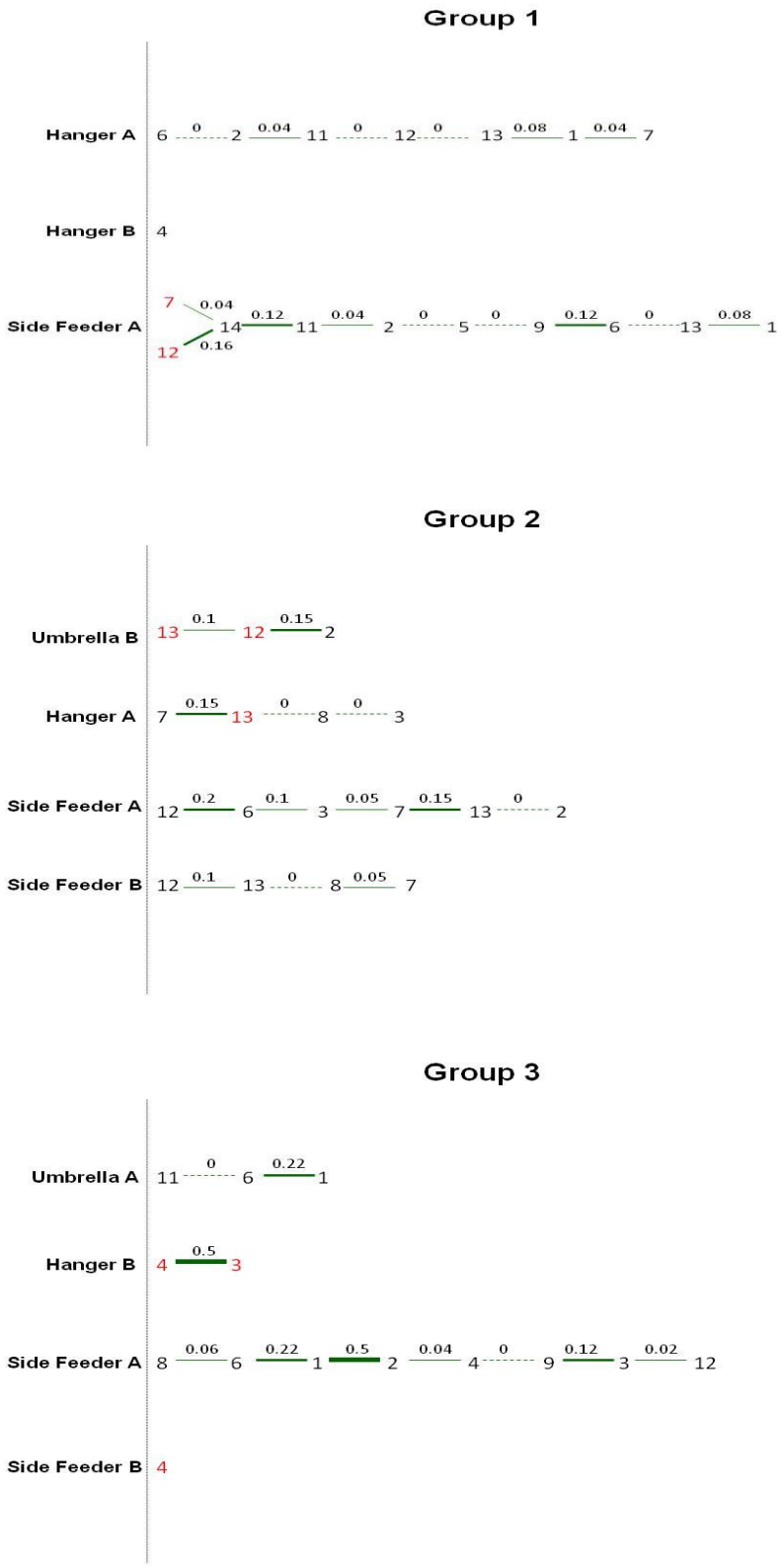


Figure 6.3: Group members' order of feeding at each novel foraging patch (from left to right, first to last bird to feed). Association strength (proportion of time spent in close proximity) between one bird and the next indicated by line weight and text above line. Demonstrators depicted in red.

The rate at which approaching and/or feeding behaviour spread through a particular group at a particular patch was sometimes rapid. For example, in Group 1, between 160 and 260 seconds into the presentation of the 'Side Feeders', five birds approached 'Side Feeder *a*' for the first time; whilst in Group 2, between 950 and 1250 seconds into the presentation of the 'Side Feeders', five birds fed at 'Side Feeder *a*' for the first time. However, this was not always the case. In Group 2, for instance, the third and fourth birds to feed for the first time at 'Hanger *a*' were separated by a period of more than 2000 seconds.

Generally speaking, the latencies between one bird and the next approaching a given patch were somewhat shorter than those between one bird and the next feeding at a given patch (Fig. 6.4, 6.5).

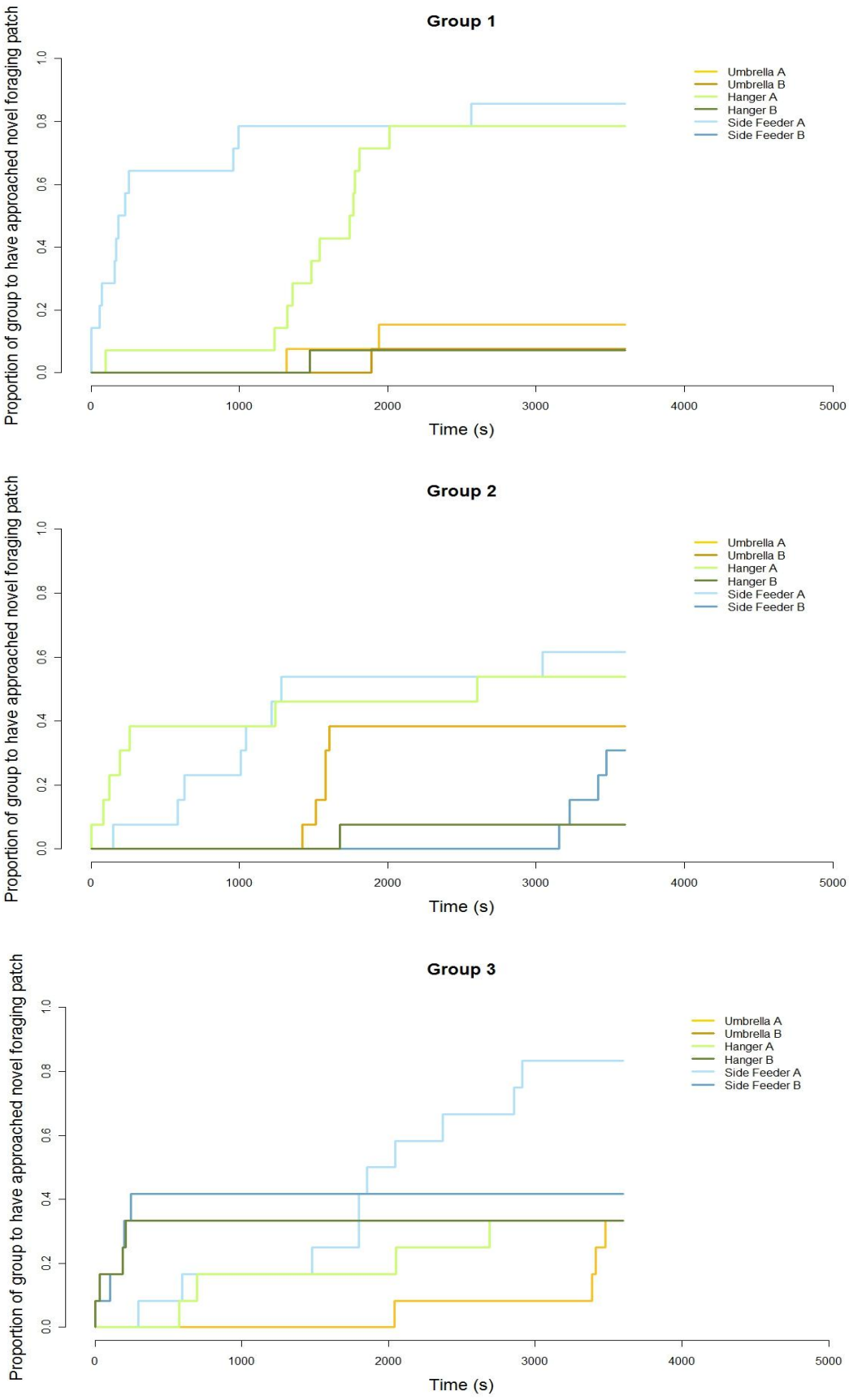


Figure 6.4: Birds' time to first approach six different foraging patches (demonstrators included).

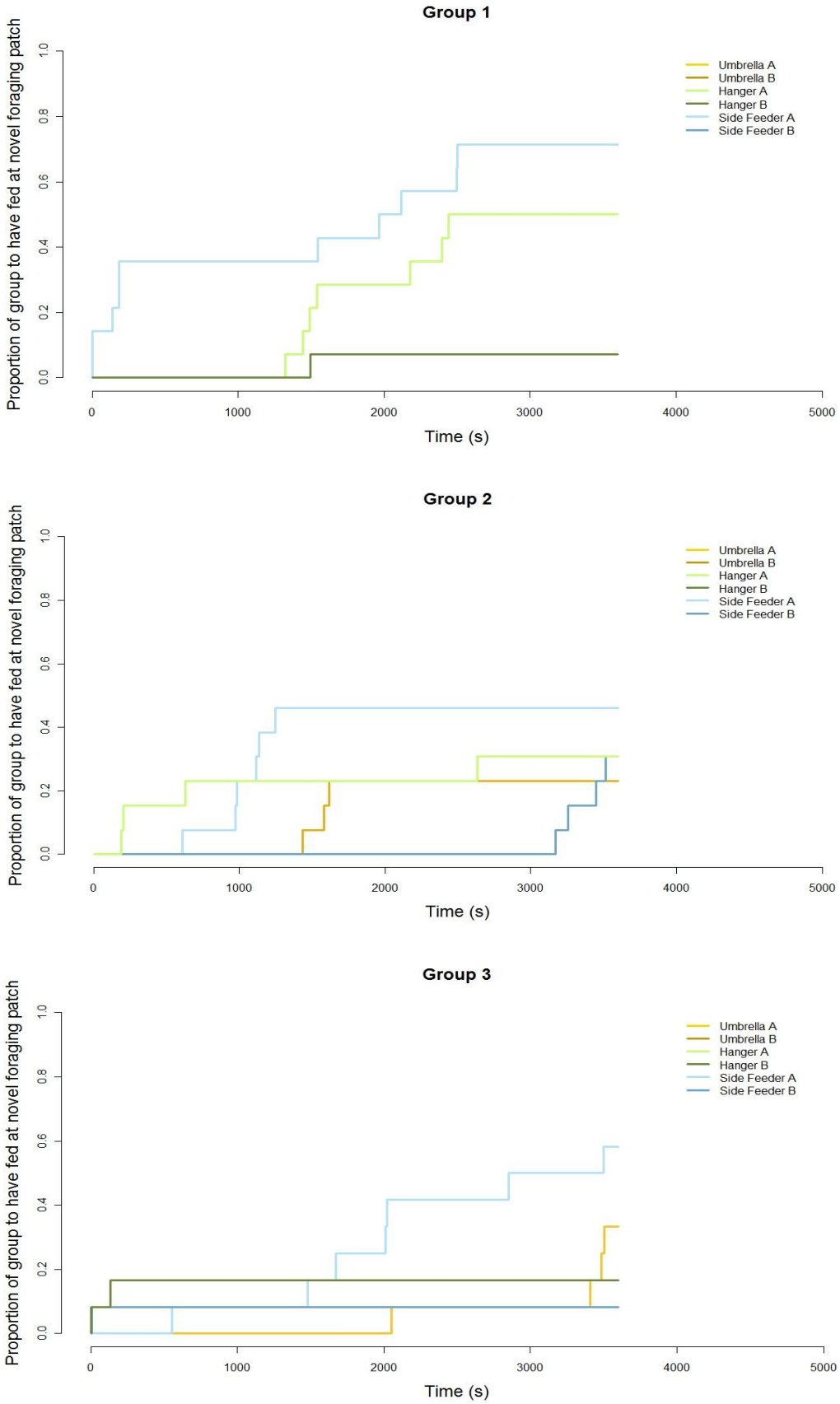


Figure 6.5: Birds' time to first feed at six different foraging patches (demonstrators included).

Evidence for Social Transmission Following Association Networks

Separate *TADA* models run for each group and foraging patch in turn produced little evidence for the network-based social transmission of approach behaviour towards patches. Indeed, all null models (models that did not allow for the possibility of network-based social transmission) received greater support than their respective social models (models that did allow for the possibility of network-based social transmission) (Table 6.1, Fig. 6.6).

When all groups and foraging patches were analysed collectively, a simple null model that contained no individual-level variables received 3.86x more support than a model that included social transmission (difference in AICc = 2.7). Indeed there was no evidence for network-based social transmission of approach behaviour, with the maximum likelihood estimator (MLE) for social transmission = 0 (LRT: Chi-sq = 0; df = 1, p = 1; 95% CI = [0, 1.42]).

A null model that contained the individual-level variables age and sex received 4.26x more support than a model that included social transmission (difference in AICc = 2.9). There was no evidence for network-based social transmission of approach behaviour, with the maximum likelihood estimator (MLE) for social transmission = 0 (LRT: Chi-sq = 0; df = 1, p = 1; 95% CI = [0, 2.14]). There was some evidence that the individual-level variables age (MLE = -0.23) and sex (MLE = 0.38) influenced birds' latencies to first approach patches, with one-year-old birds and male birds seemingly being somewhat quicker to first approach them than two-year-old birds and females.

Table 6.1: TADA results (based on groups' actual association networks) for birds' first approach times at six different novel foraging patches. Groups that contained demonstrators pre-trained to visit a particular patch are denoted 'D'. Instances in which no more than one naïve bird approached a given patch were unsuitable for analysis and are denoted 'NA'.

Group	**Foraging Patch**	**Maximum Likelihood Estimator (social transmission)**	**Null model AICc minus social model AICc)**	**Support for null model relative to social model**
1, *D*	Umbrella A	0	-4.08	7.71x
1	Umbrella B	*NA*	*NA*	*NA*
1	Hanger A	0.58	-2.28	3.13x
1	Hanger B	*NA*	*NA*	*NA*
1, *D*	Side Feeder A	0	-3.21	4.98x
1	Side Feeder B	*NA*	*NA*	*NA*
2	Umbrella A	*NA*	*NA*	*NA*
2, *D*	Umbrella B	0	-1.24	1.86x
2, *D*	Hanger A	0	-6.67	28.04x
2	Hanger B	*NA*	*NA*	*NA*
2	Side Feeder A	0.79	-0.24	1.13x
2	Side Feeder B	0	-3.73	6.46x
3	Umbrella A	0.98	-4.38	8.91x
3	Umbrella B	*NA*	*NA*	*NA*
3	Hanger A	0	-9.34	106.70x
3, *D*	Hanger B	0	-1.23	1.85x
3	Side Feeder A	0.55	-2.78	4.01x
3, *D*	Side Feeder B	0	-1.21	1.83x

Separate *TADA* models run for each group and foraging patch in turn also produced little evidence for the network-based social transmission of feeding behaviour at patches. Indeed, in only one case (Group 3, 'Side Feeder *a*') did support for the social model marginally outweigh support for the null model. In all others, null models received greater support than their respective social models (Table 6.2, Fig. 6.6).

When all groups and foraging patches were analysed collectively, a simple null model that contained no individual-level variables received 5.10x more support than a model that included social transmission (difference in AICc = 3.26). Indeed there was no evidence for network-based social transmission of feeding behaviour, with the maximum likelihood estimator (MLE) for social transmission = 0 (LRT: Chi-sq = 0; df = 1, p = 1; 95% CI = [0, 0.64]).

A null model that contained the individual-level variables age and sex received 6.39x more support than a model that included social transmission (difference in AICc = 3.71). There was no evidence for network-based social transmission of feeding behaviour, with the maximum likelihood estimator (MLE) for social transmission = 0 (LRT: Chi-sq = 0; df = 1, p = 1; 95% CI = [0, 0.15]). There was some evidence that the individual-level variables age (MLE = -0.76) and sex (MLE = 0.43) influenced birds' latencies to first feed at patches, with one-year-old birds and male birds seemingly being somewhat quicker to first feed than two-year-old birds and females.

Table 6.2: TADA results (based on groups' actual association networks) for birds' first feeding times at six different novel foraging patches. Groups that contained demonstrators pre-trained to visit a particular patch are denoted 'D'. Instances in which no more than one naïve bird fed at a given patch were unsuitable for analysis and are denoted 'NA'. Instances in which the null model received less support than the social model are indicated in bold text.

Group	**Foraging Patch**	**Maximum Likelihood Estimator (social transmission)**	**Null model AICc minus social model AICc)**	**Support for null model relative to social model**
1, *D*	Umbrella A	*NA*	*NA*	*NA*
1	Umbrella B	*NA*	*NA*	*NA*
1	Hanger A	0.045	-3.99	7.35x
1	Hanger B	*NA*	*NA*	*NA*
1, *D*	Side Feeder A	0	-3.74	6.49x
1	Side Feeder B	*NA*	*NA*	*NA*
2	Umbrella A	*NA*	*NA*	*NA*
2, *D*	Umbrella B	0	-7.70	46.99x
2, *D*	Hanger A	0	-7.01	33.28x
2	Hanger B	*NA*	*NA*	*NA*
2	Side Feeder A	0	-4.90	11.59x
2	Side Feeder B	0.71	-0.62	1.36x
3	Umbrella A	0.29	-2.96	4.40x
3	Umbrella B	*NA*	*NA*	*NA*
3	Hanger A	*NA*	*NA*	*NA*
3, *D*	Hanger B	*NA*	*NA*	*NA*
3	Side Feeder A	**0.98**	**1.02**	**0.60x**
3, *D*	Side Feeder B	*NA*	*NA*	*NA*

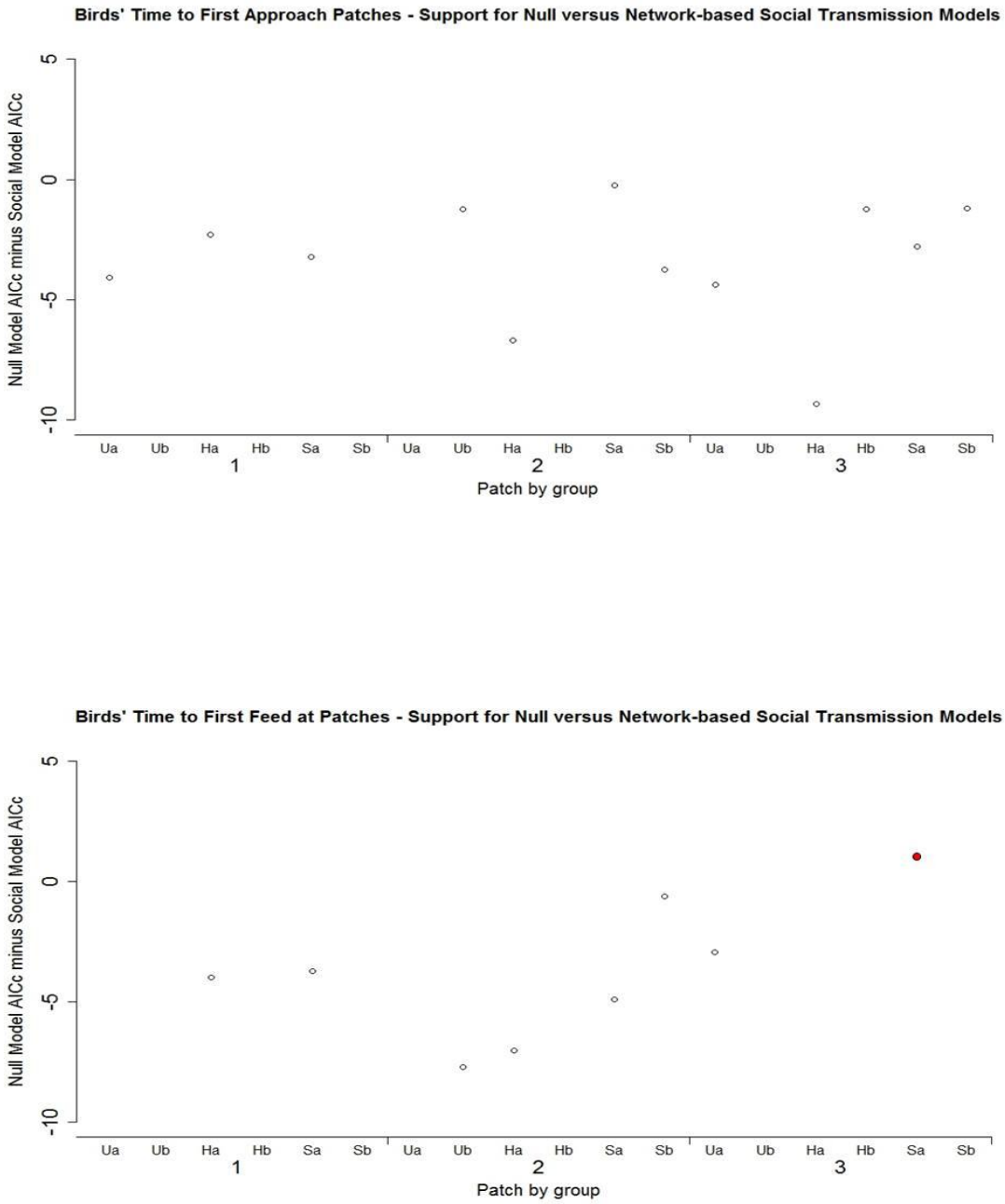


Figure 6.6: Support for null model relative to network-based social transmission model in TADAs run separately for each group and foraging patch. (When the difference in AICc between null and social models was a positive number, the null model received less support than the social model, and is indicated by a red dot.) U a/b = Umbrella a/b; H a/b = Hanger a/b; S a/b = Side Feeder a/b.

Evidence for Social Transmission Assuming Equal Connectedness across Networks

Separate *TADA* models run for each group and foraging patch in turn produced little evidence for the social transmission of approach behaviour towards patches. In only one case (Group 2, 'Side Feeder *a*') did support for the social model marginally outweigh support for the null model. In all others, null models (models that did not allow for the possibility of social transmission) received greater support than their respective social models (models that did allow for the possibility of social transmission) (Table 6.3, Fig. 6.7).

When all groups and foraging patches were analysed collectively, a simple null model that contained no individual-level variables received 3.58x more support than a model that included social transmission (difference in AICc = 2.55). Indeed there was no evidence for a general social influence on birds' latencies to approach patches, with the maximum likelihood estimator (MLE) for social transmission = 0 (LRT: Chi-sq = 0; df = 1, p = 1; 95% CI = [0, 0.31]).

A null model that also contained the individual-level variables age and sex received 4.05x more support than a model that included social transmission (difference in AICc = 2.8). There was no evidence for a general social influence on birds' latencies to approach patches, with the maximum likelihood estimator (MLE) for social transmission = 0 (LRT: Chi-sq = 0; df = 1, p = 1; 95% CI = [0, 1.88]). There was some evidence that the individual-level variables age (MLE = -0.26) and sex (MLE = 0.40) influenced birds' latencies to first feed at patches, with one-year-old birds and

male birds seemingly being somewhat quicker to first feed than two-year-old birds and females.

Table 6.3: TADA results (based on equal connectedness networks) for birds' first approach times at six different novel foraging patches. Groups that contained demonstrators pre-trained to visit a particular patch are denoted 'D'. Instances in which no more than one naïve bird approached a given patch were unsuitable for analysis and are denoted 'NA'. Instances in which the null model received less support than the social model are indicated in bold text.

Group	**Foraging Patch**	**Maximum Likelihood Estimator (social transmission)**	**Null model AICc minus social model AICc)**	**Support for null model relative to social model**
1, *D*	Umbrella A	0	-4.08	7.71x
1	Umbrella B	*NA*	*NA*	*NA*
1	Hanger A	0.22	-1.08	1.72x
1	Hanger B	*NA*	*NA*	*NA*
1, *D*	Side Feeder A	0	-3.05	4.60x
1	Side Feeder B	*NA*	*NA*	*NA*
2	Umbrella A	*NA*	*NA*	*NA*
2, *D*	Umbrella B	0	-1.24	1.86x
2, *D*	Hanger A	0	-6.22	22.42x
2	Hanger B	*NA*	*NA*	*NA*
2	Side Feeder A	**0.91**	**0.358**	**0.84x**
2	Side Feeder B	0	-3.35	5.34x
3	Umbrella A	0.78	-4.71	10.54x
3	Umbrella B	*NA*	*NA*	*NA*
3	Hanger A	0	-9.97	145.91x
3, *D*	Hanger B	0	-1.23	1.85x
3	Side Feeder A	0.24	-1.42	2.03x
3, *D*	Side Feeder B	0	-1.40	2.01x

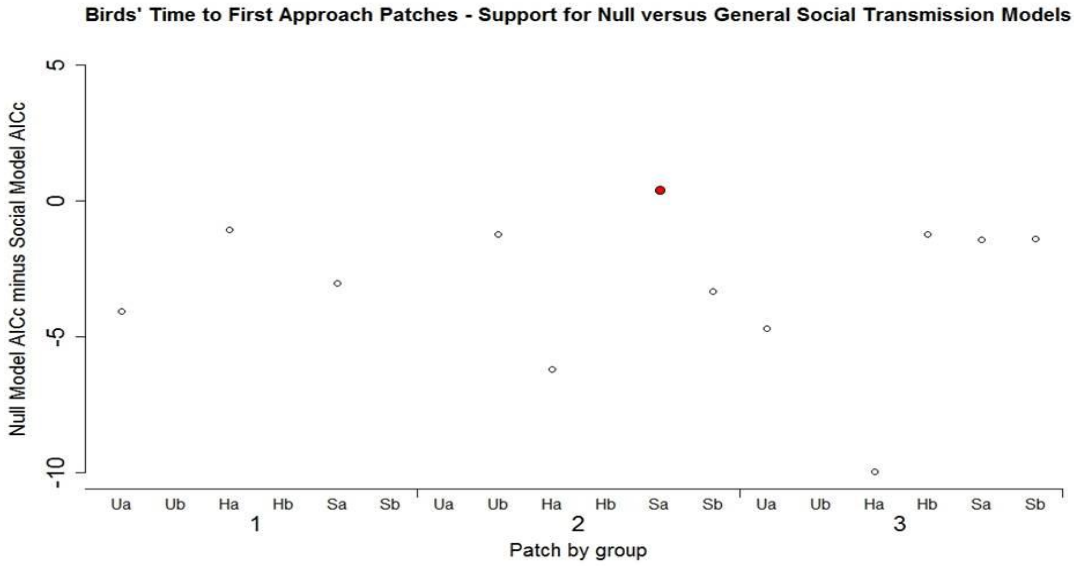
Separate *TADA* models run for each group and foraging patch in turn also produced little evidence for the social transmission of feeding behaviour at patches. Indeed, in only two cases (Group 2, 'Side Feeder *b*', and Group 3, 'Side Feeder *a*') did support for the social model marginally outweigh support for the null model. In all others, null models received greater support than their respective social models (Table 6.4, Fig. 6.7).

When all groups and foraging patches were analysed collectively, a simple null model that contained no individual-level variables received 5.08x more support than a model that included social transmission (difference in AICc = 3.25). Indeed there was very little evidence for a general social influence on birds' latencies to feed at patches, with the maximum likelihood estimator (MLE) for social transmission = 0.005 (LRT: Chi-sq = 0.016; df = 1, p = 0.90; 95% CI = [0, 0.18]).

A null model that contained the individual-level variables age and sex received 5.29x more support than a model that included social transmission (difference in AICc = 3.33). There was little evidence for a general social influence on birds' latencies to feed at patches, with the maximum likelihood estimator (MLE) for social transmission = 0.055 (LRT: Chi-sq = 0.37; df = 1, p = 0.54; 95% CI = [0, 0.38]). There was some evidence that the individual-level variables age (MLE = -0.88) and sex (MLE = 0.62) influenced birds' latencies to first feed at patches, with one-year-old birds and male birds seemingly being somewhat quicker to first feed than two-year-old birds and females.

Table 6.4: TADA results (based on equal connectedness networks) for birds' first feeding times at six different novel foraging patches. Groups that contained demonstrators pre-trained to visit a particular patch are denoted 'D'. Instances in which no more than one naïve bird fed at a given patch were unsuitable for analysis and are denoted 'NA'. Instances in which the null model received less support than the social model are indicated in bold text.

Group	**Foraging Patch**	**Maximum Likelihood Estimator (social transmission)**	**Null model AICc minus social model AICc)**	**Support for null model relative to social model**
1, *D*	Umbrella A	*NA*	*NA*	*NA*
1	Umbrella B	*NA*	*NA*	*NA*
1	Hanger A	0.12	-3.71	6.39x
1	Hanger B	*NA*	*NA*	*NA*
1, *D*	Side Feeder A	0	-3.49	5.73x
1	Side Feeder B	*NA*	*NA*	*NA*
2	Umbrella A	*NA*	*NA*	*NA*
2, *D*	Umbrella B	0	-7.70	46.99x
2, *D*	Hanger A	0	-7.01	33.28x
2	Hanger B	*NA*	*NA*	*NA*
2	Side Feeder A	0	-4.62	10.07x
2	Side Feeder B	**0.92**	**0.93**	**0.63x**
3	Umbrella A	0.15	-4.44	9.19x
3	Umbrella B	*NA*	*NA*	*NA*
3	Hanger A	*NA*	*NA*	*NA*
3, *D*	Hanger B	*NA*	*NA*	*NA*
3	Side Feeder A	**0.99**	**1.15**	**0.56x**
3, *D*	Side Feeder B	*NA*	*NA*	*NA*



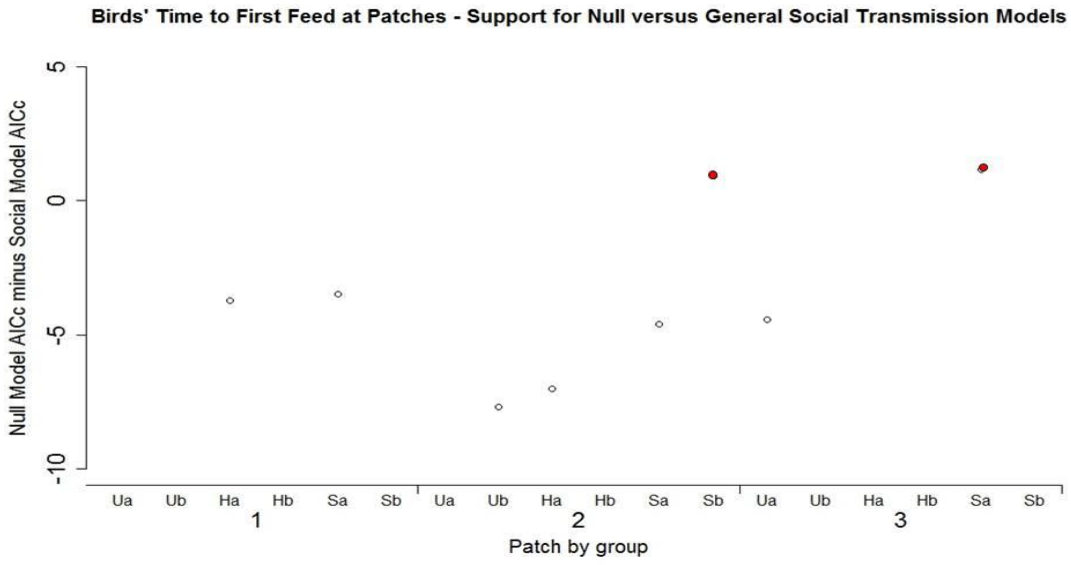


Figure 6.7: Support for null model relative to general social transmission model in TADAs run separately for each group and foraging patch. (When the difference in AICc between null and social models was a positive number, the null model received less support than the social model, and is indicated by a red dot.) U a/b = Umbrella a/b; H a/b = Hanger a/b; S a/b = Side Feeder a/b.

Discussion

In this study, I assessed the importance of budgerigars' social networks in predicting the order and latency with which birds first approached and first fed at novel, visually distinctive foraging patches.

Predictions 1, 2 and 3

Counter to my first prediction, I found little evidence to suggest that birds' first approach and first feeding times at new foraging patches were influenced by their association patterns, and that individuals with a high level of association to one another were more likely to feed at a patch in succession, and with more similar latencies, than were birds that had a low level of association (Fig. 6.2, 6.3). This was the case across different types of foraging patch, and both when groups contained demonstrators and when they did not contain demonstrators. This held true even if results from Group 1, Umbrella Patch *a* (at which demonstrators failed to approach or feed, and in which case any influence they had on their groups' uptake of novel foraging behaviour may therefore have been abnormally low) were ignored (Table 6.1, 6.2).

Counter to my second prediction, I also found little evidence of a general social influence on birds' latencies to first approach and first at feed at new foraging patches (i.e., a clustering of timings, as opposed to widely and/or evenly spaced timings between one bird and the next first approaching or first feeding at a patch), assuming all members of a group were equally well connected and paid equal attention to one

another (Fig. 6.4, 6.5). Again, this was the case across different types of foraging patch, and both when groups contained demonstrators and when they did not contain demonstrators (again, the result held true even if results from Group 1, Umbrella Patch *a* were ignored) (Table 6.3, 6.4).

Although neither my network-based nor general *TADA* models produced much evidence of social transmission of approach towards, or feeding at, novel foraging patches, this evidence was typically even weaker in those models that took into account birds' association patterns, as well as the timing of their patch visits (the network-based models), than in those that assumed all birds shared an equal level of connectedness, and considered only the timing of their patch visits (the general models). Thus, birds did not appear to pay more attention to, and/or be more inclined to follow their close associates to a given patch, than they were to pay attention to, and/or follow other, less closely associated birds.

I further found that support for null models containing the variables age and sex, when compared to their equivalent social transmission model, was typically relatively even greater than support for simple null models (that did not contain any individual-level-variables) compared to the same social transmission model. Thus, not only did birds' approach and feeding latencies show little evidence of clustering or of following their group's social network, but birds' age and sex appeared to play some part in determining the times at which they first visited foraging patches. This finding was therefore somewhat consistent with my third prediction, which was that birds' latencies to visit patches for the first time would be determined not only by network-based social transmission, but also, partly by differences in individual character traits.

Birds that were one year old tended to be quicker to first approach and first feed at patches than were birds that were two years old, whilst male budgerigars tended to first approach and first feed at patches more rapidly than female budgerigars (though neither of these effects appeared to be particularly strong).

On the basis of my findings, it is possible that birds discovered, approached and fed at patches independently of one another, and that their foraging choices were not influenced by those of their group mates (i.e., that no social transmission of information occurred). It is also possible that younger birds may have typically been somewhat more active and exploratory than older birds, making them likely to approach and feed at novel foraging patches in a shorter space of time than older birds. The same may be true of male budgerigars in comparison to female budgerigars – male budgerigars, when pair bonded, sometimes forage on behalf of their mates and provision them with food.

Indeed, the pair bonded nature of budgerigars' social groups may have been one reason behind the lack of evidence my results produced for the social transmission of first approach and first feeding times at novel foraging patches. A number of budgerigars in each group were highly bonded, usually in male-female pairs. Sometimes, highly bonded birds appeared to follow one another to food patches. For example, in Group 1, Bird 8 and Bird 9 – birds that were seen in close proximity to one another on 50% of sampling occasions during the collection of group social network data – approached 'Hanger *a*' within 10 seconds of one another during its presentation. On other occasions, however, only one member of a particular pair of highly bonded birds visited a patch. In Group 2, for example, Bird 3 (a male) fed at

both ‘Hanger *a*’ and ‘Side Feeder *a*’, but Bird 4 (a female), with whom it had been seen in close proximity on 50% of sampling occasions during the collection of group social network data, never fed at either of these patches. Pair bonded budgerigars are known to engage in courtship feeding (the regurgitation of seeds by one bird, typically the male, into the mouth of another, typically the female – see Chapter Two for further details), and I frequently observed pair bonded birds within the groups of budgerigars used in this study engaged in this activity. This raised the possibility that on occasions when one member of a pair but not the other approached and then fed at a patch, the bird that had fed may have returned to its mate and proceeded to provision it with regurgitated seeds, effectively preventing the latter from needing to access the patch itself in order to obtain food. Unfortunately, I cannot be certain of this because cameras were trained only on foraging patches and their immediate surroundings during experimental trials, and thus were unable to capture birds’ activities within the rest of their cage. Nonetheless, in budgerigar groups, unlike groups of foraging tits (Aplin *et al.*, 2012), or humpback whales (Allen *et al.*, 2013), it may be the case that new foraging behaviour is actually *less* likely to be transmitted between closely associating birds than it is to spread among birds sharing weaker social bonds. (It may also at least partially explain why not all budgerigars were seen to feed at the foraging patches presented to groups in Chapter Five.)

Further support for this possibility comes from a study on juvenile and adult jackdaws, *Corvus monedula* (Schwab *et al.*, 2008b), in which affiliated individuals (in the case of juveniles, sibling pairs; in the case of adults, mated pairs of birds) were found to be less likely to learn socially from one another than were non-affiliated (non-sibling pairs / non-mated) pairs of birds. Like budgerigars, affiliated jackdaws

frequently engage in food sharing, and the authors of this paper proposed that this 'tolerated scrounging' may have caused naïve birds to rely on their knowledgeable partners to procure food from them, rather than learning from them (see also Beauchamp and Kacelnik, 1991, for similar evidence in zebra finches, *Taeniopygia guttata*). Schwab *et al.* (2008b) also suggested that, since affiliates spend the majority of their time in close proximity to one another, this should increase the probability of them experiencing occurrences in their environment simultaneously; thus, it may in fact benefit them to pay more attention to spatially more distant individuals, which are more likely to encounter different foraging situations and consequently may provide social information of greater use.

Although my *TADA* results revealed little evidence either of network-based, or of general, social transmission of first approach and first feeding times at novel foraging patches through budgerigar groups, earlier findings suggested that their foraging choices might indeed be subject to social influence. In Chapter Five, I found that, when presented with two foraging patches they had not encountered before, a greater number of naïve budgerigars first fed at the same patch that pre-trained demonstrators in their group did, than first fed at the other available patch at which no demonstrators were feeding. In addition, I found that birds with existing personal knowledge of one foraging patch in a pair exhibited a greater tendency to switch to feeding first at the alternative patch (about which they had no existing personal knowledge) when their group contained some members that *did* have personal knowledge of this patch (and which, by feeding at it themselves, were able to provide the rest of their group with social information about it), than when their group did not contain any members able to provide them with social information about this alternative patch.

It is quite possible that the *TADAs* run here may have underestimated the true influence of birds' social networks on the order and latency of group members' visits to foraging patches. This was because individuals, having once visited a given patch, often then made several return visits during the course of a trial. A limitation of network-based diffusion analysis, however, is that models are only able to consider one time point (in this case, time to approach or feed at a patch) per individual. Hence, the models run in this study only took into account birds' first approach / first feeding times at patches, which may have caused them to underestimate the true amount of social transmission that occurred between group mates. If, for instance, one bird happened to make its first approach or first feed at a patch by following another during or shortly after, say, its second or third visit (rather than during or shortly after its very first visit), the two birds' first feeding times might well be separated by a wide span of time, resulting in little social transmission being detected by the *TADA* – even though, in reality, one bird's decision to visit the foraging patch for the first time might have been strongly influenced by the activity of the other bird visiting it for the second or third time.

Prediction 4

The *TADAs* run in this study provided little evidence of groups' social networks playing an important role in predicting individuals' order or latency to first approach *or* first feed at a new patch. In general, however, fewer birds fed at each novel foraging patch than approached it. Furthermore, the latencies between different individuals' first feeding times at a given patch (whether or not these individuals were close associates) tended to be more staggered than those between their first approach

times. If anything, therefore, the evidence for socially-mediated transmission of feeding behaviour at patches was even weaker than that for socially-mediated transmission of approach behaviour – a finding at least somewhat consistent with my fourth prediction, which was that any evidence of social transmission (network-based and/or general) would be stronger with respect to birds' first approach times at patches, than with respect to their first feeding times.

A likely explanation for this result was that, whilst a relatively large number of birds were able to approach each patch simultaneously with minimal competition for access to nearby perching space, the number of birds able to feed together at a patch was typically considerably more limited. Perching space on patches themselves was usually sufficient for two to three birds at most. Moreover, once at a patch, individual birds would often attempt to monopolise it, behaving aggressively towards any other birds that arrived at it and sometimes driving them away. In order to feed at a patch, then, newcomers typically either had to displace one or more existing foragers from the patch, or wait for them to finish feeding and leave. Thus, even if budgerigars were initially attracted to patches by the presence of other birds in the vicinity or engaged in feeding activity, individuals were often unable to forage at them straightaway. Indeed, competition for access to particular patches may even have caused some birds to avoid them altogether and visit available alternatives (namely, the opposite patch in a given patch pair) instead (for further details see Discussion, Chapter Five).

Conclusions

In this study, I found little evidence that the timing of budgerigars' first approaches towards, and first feeding behaviour at, novel foraging patches was subject to social transmission. This was because birds appeared to show no greater predisposition to follow group mates with whom they were closely associated to food patches, than they were to follow group mates with whom they usually spent little time. Furthermore, rather than occurring in quick succession, the latencies between one bird and another approaching or feeding at a patch for the first time were often quite lengthy. Combined, this meant that the *TADA* models carried out here were unable to detect much, if any, social transmission in the discovery and utilisation of novel foraging patches amongst budgerigars – even with respect to those patches at which knowledgeable demonstrators were feeding, and presumably providing social information about to the rest of their group, right from the beginning of trials.

This finding appears to contradict my earlier findings in Chapter Five, which suggested that birds *did* make use of social information when deciding where to forage, since they appeared to prefer to feed at the same patch that any knowledgeable demonstrators in their group were feeding at, before feeding at the alternative patch at which no demonstrators were feeding.

In reality, whilst some birds may indeed have discovered, approached and fed at patches independently of their group mates, it seems likely that the decisions of others may have been at least somewhat influenced by the activities of other birds in their group, but that the *TADAs* run here underestimated birds' use of social information.

One potential reason for this is that many individuals made several visits to foraging patches during the course of trials, giving those members of the group that had not yet visited the patch a number of opportunities to follow them. However, *TADAs* were only able to take into account each bird's first approach and first feeding times at a patch, which were sometimes separated widely in time. Competition for access to perching space on and around foraging patches is also likely to have hindered birds' access to them, and may have prevented them from approaching (and especially feeding at) them in such quick succession as they might otherwise have done.

Further Work

The greatest limitation of the *TADAs* carried out in this chapter was that they were only able to take into account one time point (in this case, time to first approach or first feed at a patch) per individual, which may have caused them to underestimate the amount social transmission that occurred between group mates during their visits to foraging patches. *NBDA*, however, is a relatively new statistical method for detecting social transmission within groups of animals (Franz and Nunn, 2009; Hoppitt *et al*., 2010), and is still in the process of development. Indeed, new, more flexible versions of the method (set in a Bayesian statistical framework), are currently being developed within the Laland research group, and I hope to be able to test my data set using these in due course.

During the analyses carried out here, I made the assumption that each member in a pair of foraging patches was entirely separate, despite the fact that both were presented concurrently, visible from anywhere within the confines of a group's cage,

and had some physical features (size, shape, and mode of access to food) in common. It is conceivable that birds generalised between the two objects, and that if an *NBDA* were to be run in which both were considered together (i.e., in which each bird's overall first approach / feeding times – whether these had been to patch '*a*' or patch '*b*' – were considered), stronger evidence for network-based transmission of information might emerge than has been found thus far. It should be noted, though, that even if such analyses did appear to yield some evidence for social transmission (i.e., patch visitations that were more closely clustered in time than was the case when birds' visits to patches '*a*' and '*b*' were analysed separately), it could be difficult to tease apart actual social transmission and birds' generalisation from one patch to another, from individuals' simple avoidance of competition at an already crowded patch leading to their individual discovery and exploitation of the alternative patch.

Ideally, then, further work might include examination of the timing of budgerigars' visitations to foraging patches that were less easily monopolised by a small number of birds than was the case with those presented in this study, and that a greater proportion of each group could potentially visit simultaneously. With the complication of inter-bird competition alleviated, it should become easier to assess birds' tendency (or lack thereof) to exploit any social information made available to them by their foraging group mates using *NBDA*.

Another useful extension of the work presented here might include the introduction of a control condition in which the sequence and timings of birds' arrival at a 'neutral' (non-food-containing) location, and/or the sequence and timings of birds' arrival at food patches they were already familiar with, were also assessed using *TADA*. The

results of these could then be compared against those obtained in relation to birds' first feeding times at novel foraging patches, in order to help tease apart budgerigars' perhaps instinctive tendency to affiliate through flocking, versus their use of other birds as a source of information pertaining to the location and availability of (new) food sources. (This study found little evidence of network-based social transmission of information through budgerigar groups, but even if it had done, its current design would not allow one to differentiate between whether birds were initially attracted to the vicinity of food patches merely by the presence of other birds – and that, once there, each bird 'discovered' it independently – or whether they were attracted to the vicinity of food patches at least partly on account of the exploration / foraging behaviour exhibited by those birds already in the vicinity of the patch (Hoppitt *et al*., 2010; Hoppitt and Laland, 2013; see also Atton *et al*., 2012 for an application of a similar control using order of acquisition diffusions analysis (*OADA*) on groups of sticklebacks, *Gasterosteous aculeatus*).)

Similar analyses run on an improved (see above) data set could also include a greater number of individual-level variables. Ideally, for example, null models in the analyses presented here would have contained information relating to birds' competitive rank within their group (competitive rank had previously been found to be an important predictor of budgerigars' latency to first solve a series novel foraging tasks – see Chapter Four for details). Unfortunately, though, following the amalgamation of budgerigars' original groups of seven to eight birds (Chapters Three and Four) into larger groups of 12-14 birds (Chapters Five and Six), new competitive rank data were not collected, and it was therefore not possible to include this information in the models.

Especially in cases where models that include social transmission appear to have greater support than their equivalent simple null models, the inclusion of individual-level, asocial variables in more detailed null models is necessary to rule out 'false positives', in which individuals' order and latency to perform an activity may in fact be explainable not (entirely) by social transmission, but (also) by some other factor such as an individual's rank or neophobia level. Indeed, more detailed analyses of the importance of individual-level variables in their own right in predicting individuals' latency in first approaching or feeding at a novel foraging patches (using similar methods of analyses to those used in Chapter Four to find individual-level predictors of birds' latency to first solve novel foraging tasks), might also be of use. *NBDA* itself tests only for a significant difference between an (asocial variable containing) null model and a social transmission model; while it can provide a maximum likelihood estimate for the effect of a particular asocial variable in the null model being tested, unlike a conventional Cox Proportional Hazards Model, it does not provide explicit information about whether that variable is itself a significant predictor of an individual's latency to perform an activity. Therefore, although in my experiments, age, for instance, appeared to have some effect on birds' latency to approach and feed at patches (since its inclusion in null models increased support for these relative to their equivalent social models), if considered as a predictor in its own right, it may not have been significant (in Chapter Four, although there was some support for age as a predictor of birds' latencies to solve tasks – see Table 4.2 – this was not significant), and further testing would be needed to establish this. It could also be profitable to run a non-constant-baseline rate of acquisition *TADA* (i.e., one that did not assume that the rate at which birds approached / fed at patches remained constant over time in the absence of social transmission) once this method has been fully developed.

CHAPTER SEVEN

GENERAL DISCUSSION

Principal Findings

In this thesis, I have explored a number of questions relating to the interaction between social foraging and social learning using budgerigars, *Melopsittacus undulatus*, as a test species.

In Chapter Three, I investigated the influence of scrounging on birds' acquisition of new foraging skills. I found that when birds reaped large rewards from scrounging, they were less inclined to act as producers than when they reaped small rewards from scrounging. When 'demonstrator' birds that were already competent at a particular foraging skill were inserted into groups, any positive impact they may have exerted on the spread of the new foraging skill among their naïve group mates was seemingly largely mitigated by the fact that any display of their skill (which involved solving small tasks in order to yield a food reward) not only provided naïve birds with increased scope for social learning, but also for scrounging. Upon removal of a group's demonstrator (typically its most proficient and prolific task solver), however, I found that scroungers were sometimes able to switch to become producers, particularly when scrounging had previously conferred a high level of reward. Thus, in budgerigars, it seems that scrounging may suppress immediate performance of new skills, but that it does not inhibit – in fact, may even facilitate – naïve individuals' underlying learning.

In Chapter Four, I extended my examination of producer-scrounger relationships and assessed whether certain birds were disposed to act consistently as producers, and others as scroungers – or whether birds would form skill pools, with individuals

acting as producers under some foraging circumstances, but as scroungers under others. I also measured a number of individual-level characteristics to see if any of them might serve as useful predictors of individual birds' propensities to act as producers or as scroungers. I found little evidence to suggest that budgerigars developed skill pools. Rather, certain birds appeared to consistently act as producers, while others consistently acted as scroungers. Competitive rank, sex, interaction time with, and scrounge duration from foraging tasks, were found to be useful indicators of an individual bird's propensity to adopt production behaviour. Birds of high competitive rank, and that devoted relatively large amounts of time to manipulating and interacting with tasks, were likely to solve tasks more rapidly than those of low rank, or that spent only a little time interacting with tasks. Males were also typically somewhat faster than females to initially solve tasks. By contrast, birds that spent proportionately longer scrounging from already-solved tasks tended to be slower to solve tasks by themselves than were birds that engaged in relatively less scrounging.

In Chapter Five, I examined budgerigars' use of social information when selecting foraging locations. I found that, in the absence of prior personal information, birds appeared to exploit the social information provided by knowledgeable members of their group, and typically fed at the same foraging patch as these birds, before exploring an available alternative. When all members of a group possessed uniform prior personal information about one foraging patch but lacked any prior information about another, similar, patch that was presented at the same time as it, I found that they usually visited the familiar patch before exploring the alternative. However, when a group's knowledge was split, with some birds possessing prior personal information about one patch, and others possessing prior personal information about

the other, I found that a smaller proportion of individuals visited the patch with which they were already familiar before visiting the alternative one. This suggested that some birds, at least, may have been responsive to social information provided by the foraging activities of others, even when this conflicted with their own personal information. I further found that over repeated presentations of a given pair of foraging patches, any initial group-level preferences for one member in the pair over the other (which were often relatively weak from the outset) tended to diminish as birds began to visit both patches. Thus, there was little indication that budgerigars developed enduring foraging traditions.

In Chapter Six, I used Network-based Diffusion Analysis (*NBDA*) to investigate the role of groups' social networks in predicting the order and latency of birds' visits to novel foraging patches. I found little evidence to suggest that the times at which naïve individuals first approached and first fed at the foraging patches presented in their cages, corresponded closely to the times at which other members of their group first approached and first fed at them. It is possible that birds discovered and fed at the patches independently of one another, and were not at all influenced by the activities of their group mates. Alternatively, it is possible that the *NBDAs* run in this study underestimated birds' use of social information provided by other members of their group.

Social Foraging: Opportunities and Constraints

As discussed in Chapter One, feeding in a group may interfere with an animal's ability to learn new foraging skills, or the location of new foraging patches, by itself (Giraldeau *et al*., 1994; Giraldeau and Caraco, 2000). However, it may simultaneously provide animals with the opportunity to acquire new skills or knowledge by means of social learning (Heyes, 1994; Hoppitt and Laland, 2008; Hoppitt and Laland, 2013) – something that may partially, completely, or even more than completely compensate for any potential disruption caused by social foraging to an animal's individual learning.

My findings in Chapter Three indicated that one common consequence of group foraging, namely, kleptoparasitism (scrounging), may indeed retard naïve budgerigars' deployment of new skills. However, I found no evidence that scrounging compromised their underlying learning of these skills. If anything, birds that had been given ample opportunity to scrounge appeared to be more capable of engaging in production behaviour when the need arose, than were those whose scrounging opportunities had been limited. Thus, scrounging did not appear to interfere with birds' ability to learn how to manipulate objects by themselves in order to obtain food from them. On the contrary, it seemed to increase their motivation to interact with tasks in order to access food from them when competent producers, on whom they had previously relied to provide food, were removed from their group. This may have been because scrounging from pre-solved tasks served to strengthen birds' association between the tasks in question and obtaining a food reward, causing them to interact with them more persistently (and ultimately be more likely to solve them) once

demonstrators were removed from their group, than was the case when they had reaped only small rewards from scrounging (and perhaps formed only weak associations between the task objects and food). Therefore, under some circumstances at least, it is possible that scrounging can represent as much an opportunity for learning, as it does a constraint.

Foraging as part of a group can also potentially allow naïve animals to rely on cues provided by knowledgeable ones to locate and/or assess the quality or safety of new food patches. My findings in Chapter Five suggested that budgerigars were able to make use of such information, with naïve individuals typically opting to forage at the same food patches as pre-informed, knowledgeable members of their group. Although in the case of my experiments, birds in groups containing pre-informed demonstrators were on average no quicker to first visit a food patch than were birds in groups that did not contain demonstrators (in which birds had to rely on individual exploration in order to locate food patches), it seems highly likely that in the wild, where seed clusters are no doubt much more widely dispersed than was the case in my experiment, such reliance on social information may well help naïve individuals find and access food more quickly than they would if they were to ignore available social information and obtain food by means of individual exploration alone.

Social Learning Mechanisms

The studies I conducted in the course of this thesis did not explicitly examine which, if any, social learning mechanisms were employed by budgerigars when learning how

to solve novel foraging tasks or locate novel foraging patches. That said, their use of certain mechanisms seems more plausible than their use of others.

For instance, although it is possible that budgerigars may be capable of imitating one another's actions (Dawson and Foss, 1965; Heyes and Saggerson, 2002), it seems unlikely that they made use of this ability when presented with a series of novel foraging tasks in Chapter Three. Here, informal observation suggested that birds often used somewhat different techniques to access food from the same tasks. Whereas one bird might use its beak to lift the paper lid off a jar, for example, another bird might be seen to use its foot. (Note, however, that more detailed video analysis would be necessary before any solid conclusions could be drawn about the consistency with which individual budgerigars used one technique over another, or the similarity / dissimilarity between different individuals' task solving techniques, since I did not formally record the precise manner in which birds solved tasks during my original study. Such an analysis, however, could form a useful future extension of the study.) In addition, since tasks were presented to groups of eight freely interacting birds (not just to a single demonstrator and a single observer separated by a partition, as is more traditionally the case in social learning experiments), it may well have been difficult for naïve birds to obtain repeated or uninterrupted views of the exact actions used by competent birds when accessing food from tasks.

More probable social learning mechanisms utilised by budgerigars during the presentation of novel foraging tasks in Chapter Three, and of novel foraging patches during Chapter Five, include social facilitation, response facilitation, stimulus enhancement, and/or local enhancement (see Chapter One for details). Social

facilitation and/or response facilitation may have been important in initially inducing naïve birds to join knowledgeable group mates that were already accessing food from tasks (Chapter Three) or foraging at particular locations (Chapter Five). Equally, stimulus enhancement and/or local enhancement may have been important in inducing birds to begin interacting with novel tasks, and/or begin feeding at novel foraging patches.

During the presentation of novel foraging tasks in Chapter Three, it seemed possible that budgerigars may have learnt as much from interacting with the products of skilled group mates' behaviour (i.e., foraging from already-solved tasks) as they did from direct observation of skilled group mates' task solving activities. This was because although naïve birds sometimes scrounged by displacing knowledgeable ones from recently solved tasks (which naïve birds might conceivably have witnessed being solved), they often arrived at, and scrounged from, tasks well after the producer had left (any birds that they displaced from tasks being fellow scroungers, not skilled producers). Therefore, it may have been the reinforcement birds received by acquiring food from particular objects at particular locations, made available via another bird's labour, which motivated them to subsequently explore and in some cases successfully produce food from unsolved tasks by themselves (similar to the case of British tits learning to open milk bottle tops in the mid-twentieth century (Fisher and Hinde, 1949; Hinde and Fisher, 1951; Sherry and Galef, 1984), and of Israeli black rats learning to strip pine cones (Zohar and Terkel, 1991; Aisner and Terkel, 1992; Terkel, 1996; Hoppitt *et al.*, 2008)). Indeed, had birds had greater opportunity to observe individual producers in action, it is possible that, rather than learning to associate particular objects with food, they might have instead learnt to associate particular

individuals with food – and that this might in fact have compromised their ability to learn new foraging skills.

Social Learning Strategies

Natural selection ought to have favoured transmission biases or specific adaptive social learning strategies that dictate the contexts under which individuals will rely on information provided by others, instead of learning by themselves (Boyd and Richerson, 1988). Animals should be selective with regard to when, and from whom, they use social information, and what they learn (Laland, 2004; Hoppitt and Laland, 2013).

In Chapter Five of this thesis, I investigated budgerigars' potential use of an 'approach others / feed in the same location as others when uncertain' strategy when locating food. Consistent with the implementation of such a strategy, I found that, when birds lacked any prior personal information about available foraging patches, they appeared to exploit the social information provided by knowledgeable members of their group, and tended to feed at the same patch as these birds before exploring the other available patch. I also found that, when all members of a group possessed uniform prior personal information about one foraging patch but not the other, they usually visited this patch before exploring the other one. However, when a group's knowledge was split, with some birds possessing prior personal information about one patch, while others in the group possessed prior personal information about the other, I found that a smaller proportion of individuals (relative to when birds possessed

uniform prior personal information) visited the patch with which they were already familiar before visiting the alternative one. This suggested that some birds, at least, remained responsive to social information provided by the foraging activities of others, even when this conflicted with their own personal information. This again was consistent with (at least some) birds following an 'approach others / feed in the same location as others when uncertain' rule and weighting current social information provided by group mates that had already begun to forage during a particular trial, above potentially outdated personal information gathered during preceding trials or pre-training.

In Chapter Six, I used Network-based Diffusion Analysis (*NBDA*) to explore the possibility that budgerigars might engage in 'directed social learning' (Coussi-Korbel and Fragaszy, 1995), being relatively more likely to follow, or learn from, individuals with whom they were closely associated than they were to follow, or learn from birds they rarely interacted with. I found little evidence of this being the case, but it is possible that this null result may have been largely due to limitations in the methods of analysis used here. Additional work is needed in order to investigate this question further.

Future Directions

Numerous aspects of social foraging in budgerigars, and other species, remain to be tested. Indeed, I have already undertaken a further set of experiments investigating producer-scrounger dynamics and the effect of scrounging on the spread of novel task

solving behaviour in groups of captive ravens, *Corvus corax*, and carrion crows, *Corvus corone*, which, once analysed, I hope to be able to compare against my findings from the similar set of experiments I conducted with budgerigars in Chapter Three of this thesis.

These additional experiments were carried out at the Haidlhof research facility at the University of Vienna, and involved one group of ravens (10 individuals) and one group of carrion crows (12 individuals), both of which were sequentially presented with multiple copies of four different types of novel foraging task. As with the experiments I conducted with the budgerigars, two of the tasks I presented to the corvid groups were loaded with small quantities of food (one segment of Frolic Complete® dog biscuit) that restricted scrounging opportunities, and two were loaded with larger quantities of food (five segments of Frolic Complete® dog biscuit), permitting greater opportunity for non task-solving birds to scrounge from members of their group that successfully produced food from the tasks. In other respects, though, the experiments I ran with the corvids differed somewhat from those that I had previously run with the budgerigars.

Firstly, unlike in my budgerigar experiments, I did not seed the corvid groups with any pre-trained demonstrators at the beginning of any task presentations. This removed the problem of groups containing more birds during the presentation of some tasks than during the presentation of others, and of demonstrators potentially altering their group's dynamics and/or increasing competition for access to tasks. Secondly, I no longer simply removed one producer at a fixed point in proceedings (in the case of my experiments with the budgerigars, this had been the demonstrator bird at the end

of trial 7) to assess what effect this would have on the remaining group members' producing and scrounging activity. Rather, I ran trials with all group members present until such a point as when two consecutive trials had passed in which no new task solvers emerged. At the beginning of the following trial, I then separated the most prolific producer (task solver) in a group from the rest of its group mates, and ran the trial without this bird present. Trials continued in this fashion until a further two trials elapsed in which no new task solvers emerged. At this point, the next most prolific producer remaining in the group was also removed prior to conducting further trials. Producers were sequentially removed from groups in this manner until the point was reached at which all group members had been seen to solve at least one task, or until two trials passed in which none of the remaining birds solved any tasks at all. By removing not just one, but several, producers from each group during the course of a given series of task presentations, I hope to be able to gain greater insight into the effect of restricted versus less-restricted scrounging opportunities on the rate and extent of the uptake of production behaviour through groups of birds than was possible in the case of my experiments with budgerigars.

Another difference between my corvid and budgerigar experiments was the manner in which I exposed birds to task objects prior to the beginning of actual trials. In the case of the budgerigars, birds were given access to millet seeds inside, or in close proximity to, reduced versions of each of the four tasks they were to be presented with. Earlier experiments (run by another member of the Laland research group) had suggested this would be necessary in order for birds to be likely to solve tasks, when presented in complete form, in a reasonable timeframe. The criticism could be made, however, that this method of pre-exposure provided birds with too much prior

information about how to solve tasks, and thus may have lessened the importance of the different scrounging conditions birds encountered during actual trials, in determining birds' ability or inclination to act as task solvers. Equally, allowing birds to extract food from reduced versions of tasks may conceivably have caused them to form associations between incomplete tasks and the acquisition of a food reward, which then blocked or overshadowed their ability to successfully interact with (solve) complete versions of tasks during proper trials. During my raven and crow experiments, I avoided this potential problem by granting birds prior exposure to empty forms of each task, in order to alleviate their neophobia towards them, but not loading the tasks with food until the beginning of each group's first proper trial.

Following the collection of more data, another avenue of research that might be pursued to extend the work presented in Chapter Four of this thesis, would involve looking in more detail at the behaviour of individual birds during group foraging situations. In Chapter Four, I related a number of individual-level traits to budgerigars' performance in producer-scrounger foraging scenarios, and found that characteristics such as sex, competitive rank and propensity to interact with tasks served as useful predictors of birds' latency to act as producers for the first time. A profitable extension of this work could investigate which birds in a group, of those yet to acquire production skills, were most likely to switch from scrounging to producing if competent producers were lost or removed from their group. (Chapter Four only examined the producing behaviour of birds in trials 1-7 of a total of 10 task presentations. Competent producers were removed from groups in trials 8-10.) In trials 1-7, those birds who became producers were found typically to spend relatively little time scrounging. However, it would be interesting to see if the same applied to

those birds in the 'first wave' of new solvers following the loss of existing competent producers from groups; or whether, for instance, birds who had previously earned high rewards from scrounging were subsequently highly incentivised to access food from tasks by themselves once the need arose. Unfortunately, a lack of data (in the experiments conducted in Chapter Three, only six birds switched from operating as scroungers to operating as producers following the removal of their group's demonstrator) prevented this question from being addressed with my existing data set.

In the context of social learning strategies and birds' choice of foraging patches, which I began to examine in Chapter Five, it might be interesting to establish whether certain birds consistently favoured personal information over social information, and vice versa; and, if so, whether birds' choices could be related to such individual-level character traits as age or competitive rank.

Investigation into birds' use of social information when it indicated that foraging patches were poor to feed at (rather than good, as was always the case in the experiments conducted in Chapter Five), and/or their propensity to use social information when their own prior personal information was that a particular patch was poor to feed at (rather than good) could also be illuminating. Indeed, were birds to be presented with one patch that was consistently poor, or difficult to extract food from, compared to one that consistently yielded a good, easy-to-access supply of food, it might be the case that, rather than gradually dispersing to feed at both patches (as happened over time in Chapter Five), groups could actually develop 'traditions' and consistently favour one patch over the other. The strength and longevity of these

could then potentially be tested by sequentially removing informed individuals from a group and replacing them with naïve ones.

In addition, experiments in which budgerigars were allowed to watch demonstrations of birds foraging at particular patches, but prevented from interacting with these patches themselves (for example, by means of a Plexiglas screen) until after demonstrators had been removed from the cage, could aid in disentangling budgerigars' potential instinct simply to congregate with other birds, from their assessment of, and reliance on, social information to guide them to profitable foraging patches. Such a method could also allow birds to be shown several different demonstrations of several different foraging patches, sequentially or simultaneously, before being 'asked' to chose one over the others. Again, this would enable more in-depth analysis of the social learning strategies used by budgerigars when making foraging decisions.

In light of my finding in Chapter Six (where I used a sub-set of the data I had originally collected during Chapter Five to examine not only birds' first feeding times at patches, but also their first approach times, in order to test the prediction that the latter would be relatively more clustered in time) that fewer birds tended to actually feed at patches than initially approached them, it could also be worthwhile to re-run the analyses already conducted in Chapter Five on birds' first feeding choices, this time using their first approach choices at demonstrated / non-demonstrated patches, and at patches they did or did not possess prior personal information about. Such analyses might in fact reveal, for instance, a stronger influence of demonstrators' activities on birds' first choice of foraging patch, than was apparent from looking only

at the feeding times of those birds that managed to successfully access the patch in question. It might also aid in distinguishing between birds that appeared to try and use the social information made available to them by other members (for example, demonstrators) of their group (but were unable to successfully compete for access to the foraging patch), and birds that appeared to show no interest at all in the social information provided by other members of their group. Compared against information on birds' first approach and first feeding times at the alternative (non-demonstrated patch) in a pair, this might provide some insight into whether the first birds to pioneer visits to this, tended to be those who had first attempted to feed at the demonstrated patch, but failed, or those who had never shown any interest in feeding there, and were perhaps more independent (less influenced by social information) foragers.

With regards to the continued exploration of the importance (or lack of importance) of network-based social transmission of foraging information through budgerigar groups that was begun in Chapter Six, I propose that it could be useful to examine the spread of foraging behaviour through groups housed in considerably larger enclosures, in which not all group members, and not all foraging patches, were simultaneously visible from any one point within the enclosure. In a more naturalistic arrangement such as this, association patterns between specific birds might, after all, be revealed as useful predictors of birds' order and latency to visit novel foraging locations.

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